Observations on the systematics of the genus *Difflugia* in Britain (Rhizopoda, Protozoa).

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Contents

Synopsis

Detailed descriptions of the shell structure in thirty-eight species of *Difflugia* are given, and further information on one species which has been redescribed in an earlier report (Ogden & Fairman, 1979) is included. Two new species, *Difflugia hiraethogii* and *D. stoutii,* are described, and other systematic changes include the following new combinations: *D. cylindrus* (Thomas, 1953), *D. lacustris* (Penard, 1899), *D. microclaviformis* (Kourov, 1925), *D. microstoma* (Thomas, 1954), *D. parva* (Thomas, 1954), *D. tenuis* (Penard, 1890), *D. tricornis* (Jung, 1936), *D. venusta* (Penard, 1902) and *D. distenda* nom, nov., *D. gassowskii* nom, nov., *D. paulii* nom. nov., *D. rotunda* nom. nov. Seventeen of these redescriptions are new records for the British Isles. The structure of the shell is discussed and the patterning of the organic cement which binds the particles together is shown to be a useful taxonomic character.

Introduction

The taxonomy of specimens belonging to the genus *Difflugia* is based mainly on differences in size and shape of the agglutinated shells constructed by these animals. Comparison of cytoplasmic features are either difficult or impossible because most of it is encased by the shell which is often opaque. Differences in the shell features have resulted in about three hundred named species, varieties and forms being currently attributed to the genus. This proliferation of species is due to a combination of the lack of good diagnostic features and inadequate descriptions. The problem is clearly shown in the only comprehensive survey of the genus, based on African specimens, by Gauthier-Lièvre and Thomas (1958). In this work the authors had difficulties with several groups of individuals which shared common features, and as a result, about half of the 129 species described were designated as varieties or forms.

Some earlier studies (Ogden, 1979, 1980; Ogden & Fairman, 1979) were concerned with the variation of specimens having a pyriform shell, and the surface

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ultrastructure as revealed by the scanning electron microscope. The results showed that there was usually a limited variation in size, shape and composition of the shell within a species, whilst in some instances the patterning of the organic cement which binds the particles together was a reliable specific character. The present account uses the experience gained from these previous studies to extend the examination of shell structure in *Difflugia,* and to establish specific features for ten of the varieties of *Difflugia oblonga* listed by Gauthier-Lièvre and Thomas (1958). Thirty nine species are described, of which some are new records for the British Isles. Some 600 specimens have been examined and over 3000 micrographs representing different aspects of the shells are retained in the Protozoa Section, Department of Zoology as part of the study collection.

Materials and methods

Samples have been collected from several localities in England and Wales during the last four years. The material gathered varied from mosses, water plants including the substrate associated with the roots, and clumps of algae. Type of habitat ranged from areas of bog, banks of streams and small ponds in the New Forest, Lake District and North Wales to the dykes and rivers of Norfolk and Suffolk. Information relating to locality, date and type of sample is given with the description of each species as several have been found in more than one habitat.

Specimens of *Difflugia* were selected by searching through small isolates of material in a petri dish. Specimens were extracted using a glass micropipette, washed in several transfers through distilled water, and then individual shells were manipulated with a single-hair brush onto a small drop of Araldite on a previously cleaned cover slip. When about twenty specimens were positioned on each cover slip it was glued with Araldite onto a standard aluminium stub. In a few instances the very small delicate specimens collapsed before or during manipulation, this problem was overcome by transferring the washed specimens in a small drop of water onto cleaned cover slips and allowing it to dry. Prepared stubs were coated evenly with gold or gold/palladium, using a conventional sputter coating device, and examined in a Cambridge Stereoscan S180 operating at 10kV. The results were recorded on Ilford HP5 film.

Systematic descriptions

In a previous review (Gauthier-Lièvre & Thomas, 1958) of the genus the species were divided into ten groups, namely; lobed, collared, compressed, urceolate, globose, ovoid-globose, elongate, acute angled, horned and pyriform, but no particular significance was attached to these groupings. However, it does show the diversity of shell shape that has been included in the genus. Similarly in this report the species have been grouped together, the pyriform and elongate species are described first, followed by those which are pointed or have aboral protruberances, then the ovoid or spherical and finally the two compressed species.

Pyriform and elongate species

Difflugia bryophila (Penard, 1902) Jung, 1942

Difflugia pyriformis var. *bryophila* Penard, 1902
Difflugia oblonga var. *bryophila* (Penard, 1902) Gauthier-Lièvre & Thomas, 1958

DESCRIPTION. The shell is brown, pyriform, with the sides usually tapering evenly to the aperture (Figs. 1a & d), although the occasional specimen may be slightly mis-aligned or

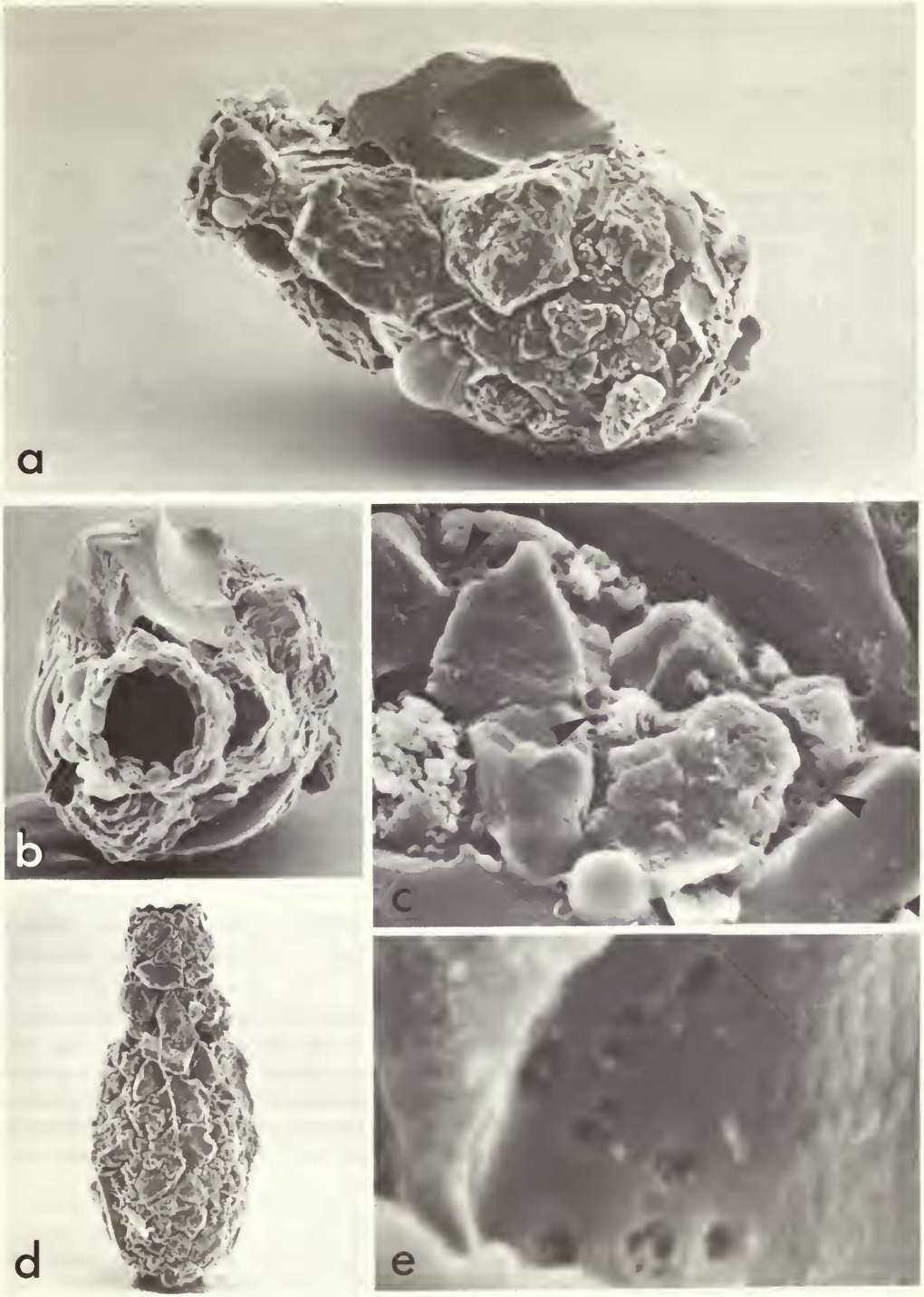

Fig. 1 *Difflugia bryophila:* a, lateral view of shell with large particles obscuring the basic outline ×780; b, apertural view ×760; c, portion of shell surface showing the distribution of organic cement (arrowed) ×5100; d, lateral view of specimen with typical basic outline ×440; e, detail of organic cement ×24 000.

Table 1 Range of measurements (in μm) of pyriform specimens.

Number of specimens	Species	Length (L)	Breadth (B)	Diameter of aperture (d)	B/L	d/L
3	*D. minutissima*	7–14	6–10	2–3		
11	*D. pulex*	28–43	21–30	7–10	0·78±0·10	0·26±0·04
19	*D. pristis*	33–42	21–31	10–13	0·69±0·08	0·31±0·03
3	*D. glans*	67–74	44–50	19–22		
36	*D. manicata*	60–88	37–54	12–20	0·61±0·04	0·20±0·02
25	*D. tenuis*	60–87	37–50	17–27	0·57±0·06	0·30±0·03
7	*D. linearis*	96–108	32–38	12–13	0·35±0·02	0·12±0·01
21	*D. gassowskii*	91–120	45–55	16–21	0·50±0·05	0·18±0·02
39	*D. bryophila*	83–141	49–67	16–22	0·55±0·07	0·17±0·02
36	*D. petricola*	96–124	61–84	20–31	0·65±0·06	0·23±0·03
*(47)	*(D. petricola)*	(108–151)	(72–99)	(25–36)	(0·62±0·05)	(0·22±0·02)
4	*D. paulii*	119–130	48–54	19–23	0·40±0·01	0·17±0·01
38	*D. lanceolata*	108–155	56–92	22–32	0·51±0·05	0·20±0·02
6	*D. parva*	131–162	61–80	19–27	0·51±0·04	0·17±0·02
23	*D. lacustris*	140–231	63–94	26–42	0·41±0·04	0·18±0·02
22	*D. cylindrus*	186–264	91–130	34–49	0·53±0·05	0·21±0·02
46	*D. viscidula*	165–284	116–215	46–89	0·75±0·09	0·30±0·04

*measurements quoted from an earlier report (Ogden & Fairman, 1979)

have a large particle obscuring the even-tapering (Fig. 1a). It is composed mainly of a mixture of small to medium pieces of quartz and the occasional diatom frustule or siliceous flagellate cyst. In common with most rough, thick shells, organic cement is seen infrequently (Fig. 1c), it appears as an open network, with a mesh about 350–450 nm in diameter. The walls of the mesh are not pronounced but blend with the matrix, the mesh openings are often covered by inner strands of cement which appear to form a smaller mesh (Fig. 1e). The aperture is circular and surrounded by small particles (Fig. 1b), in several of the specimens examined small flagellate cysts had also been incorporated to give an irregular margin.

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Mately Bog, Lyndhurst, New Forest, Hampshire in March, 1980 and at Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Belgium (Chardez & Gaspar, 1976; Couteaux, 1969), British Isles (Cash *et al.*, 1919), Chile (Jung, 1942), Congo (Chardez, 1964), Czechoslovakia (Rosa, 1957), France (Thomas, 1954), Gambia (Decloitre, 1947), Germany (Jung, 1936), Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Spain (Gracia, 1972*a*), Switzerland (Penard, 1902), Tunisia (Gauthier-Lièvre & Thomas, 1958), West Africa (Decloitre, 1948).

REMARKS. This description is in good agreement with Penard (1902) who stated that the sides were rather straight and that it was formed of stones which were usually large and angular.

Amongst the sample from Matley Bog were specimens of *Pontigulasia* which were indistinguishable in size and shape from those of *D. bryophila.* Observations of the former specimens by optical microscopy to determine the presence of an inner diaphragm, the distinguishing generic character for *Pontigulasia,* are often difficult. However, detailed examination by scanning electron microscopy showed that, unless the apertural opening is blocked, it was easy to identify the inner diaphragm and that additionally there are differences in their organic cement patterns (a review of the genus *Pontigulasia* is in preparation).

The random selection of these specimens from the sample gave a ratio of 3 : 1 in favour of *D. bryophila*.

Difflugia cylindrus (Thomas, 1953) comb. nov.

Difflugia oblonga var. *cylindrus* Thomas, 1953

DESCRIPTION. The shell is usually opaque, cylindrical, tapering evenly from the aboral region to the aperture (Fig. 2a). It is composed mainly of medium to large pieces of quartz with the occasional diatom frustule on the rough surface, but the latter are seldom incorporated into the thick structure. Small areas of organic cement in the form of a network are seen infrequently (Fig. 2d). Each mesh of the network is between 300–500 nm in diameter, has thick walls and is covered by a thin perforated layer of cement, the pores of which are evenly distributed and are about 30 nm in diameter (Figs. 2e & f). The aperture is irregular in both outline and composition, being roughly circular and usually surrounded by small particles but often incorporating medium particles that produce a jagged margin (Fig. 2b & c).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from a sample of aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Austria (Laminger, 1973*b*, 1975, 1976), Belgium (Chardez, 1980; Chardez & Gaspar, 1976), Congo (Chardez, 1964), France (Thomas, 1953, 1954; Thomas & Mabille, 1956), Germany (Voeltz-Höhn, 1971), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Moraczewski, 1965).

REMARKS. This species was initially described by Thomas (1953) as a new variety of *D. oblonga,* he also listed what he considered to be previous descriptions of this variety under the general descriptions of *D. oblonga* given by earlier workers. These are not repeated here, but suggest that this variety may be found throughout Europe. The shape, structure and size of the shell, together with the distinct patterning of the organic cement matrix as described above, are considered to be good specific characters sufficient to warrant the raising of this variety to species rank.

Difflugia gassowskii nom. nov.

Difflugia pyriformis longicollis Gassowsky, 1936
Difflugia longcollis (Gassowsky, 1936) Ogden & Hedley, 1980

DESCRIPTION. The shell is pyriform, with a distinct short neck about one-third of the body length, and a rounded aboral region (Fig. 3a). It is rough and composed of small to medium angular pieces of quartz, small areas of organic cement are sometimes seen between particles (Fig. 3b). The cement is in the form of a network, the mesh of which is about 400–550 nm in diameter and the walls 125–200 nm thick, each mesh enclosure has a covering with small perforations about 50 nm in diameter (Fig. 3c). The aperture is circular.

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and at Clocaenog Forest, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Belgium (Chardez, 1980; Couteaux, 1969), British Isles (Ogden & Hedley, 1980), Germany (Voeltz-Höhn, 1971), Netherlands (Hoogenraad & Groot, 1940a), Nigeria (Gauthier-Lièvre & Thomas, 1958), Poland (Moraczewski, 1961, 1965), Roumania (Godeanu *et al.,* 1973), Russia (Gassowsky, 1936), Spain (Gracia, 1972*a*; Margalef, 1955).

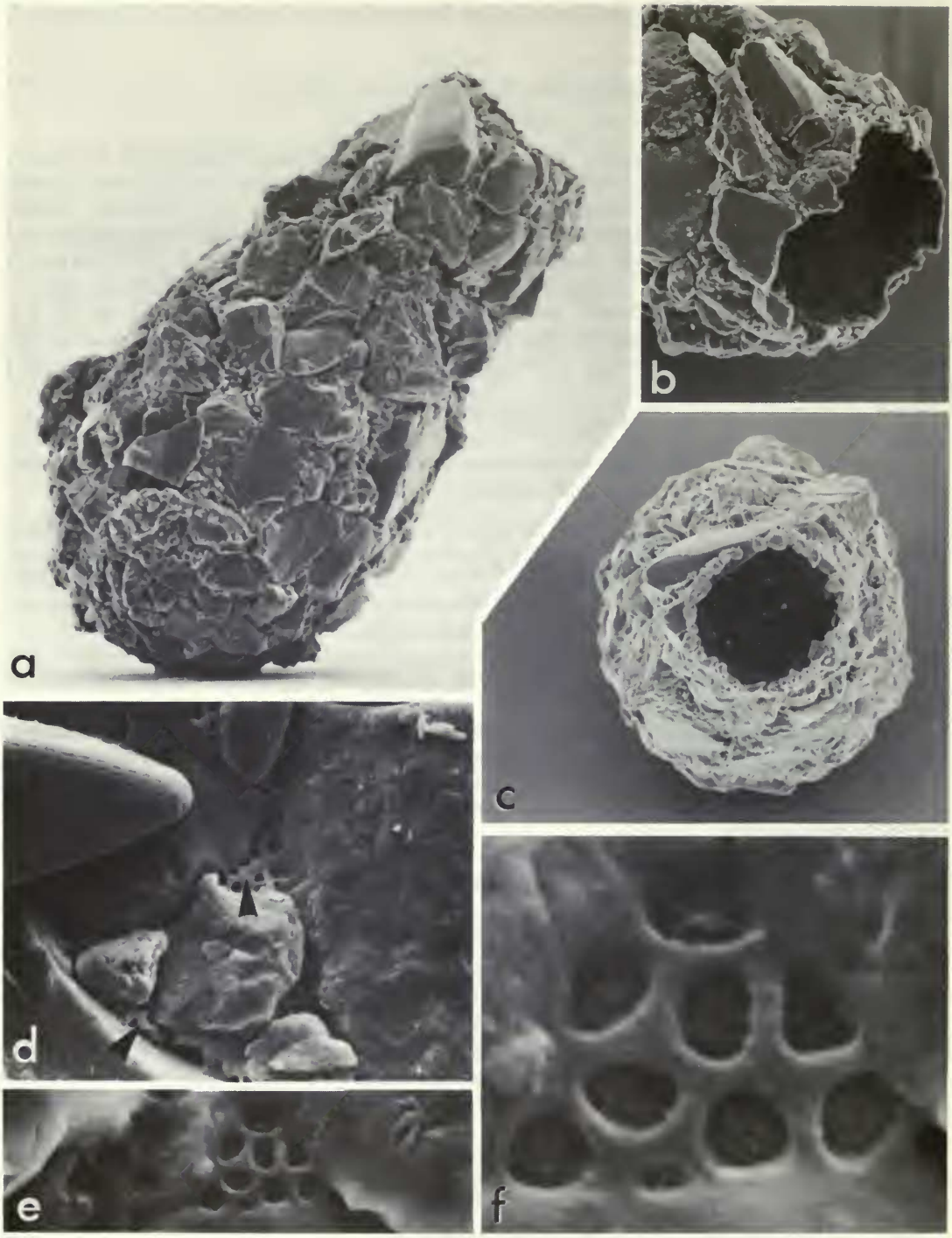

Fig. 2 *Difflugia cylindrus:* a, lateral view ×450; b, side view of aperture to illustrate the irregular margin ×770; c, apertural view ×410; d, shell surface with areas of organic cement (arrowed) ×4200; e, typical arrangement of organic cement network ×8700; d, detail of organic cement ×27 000.

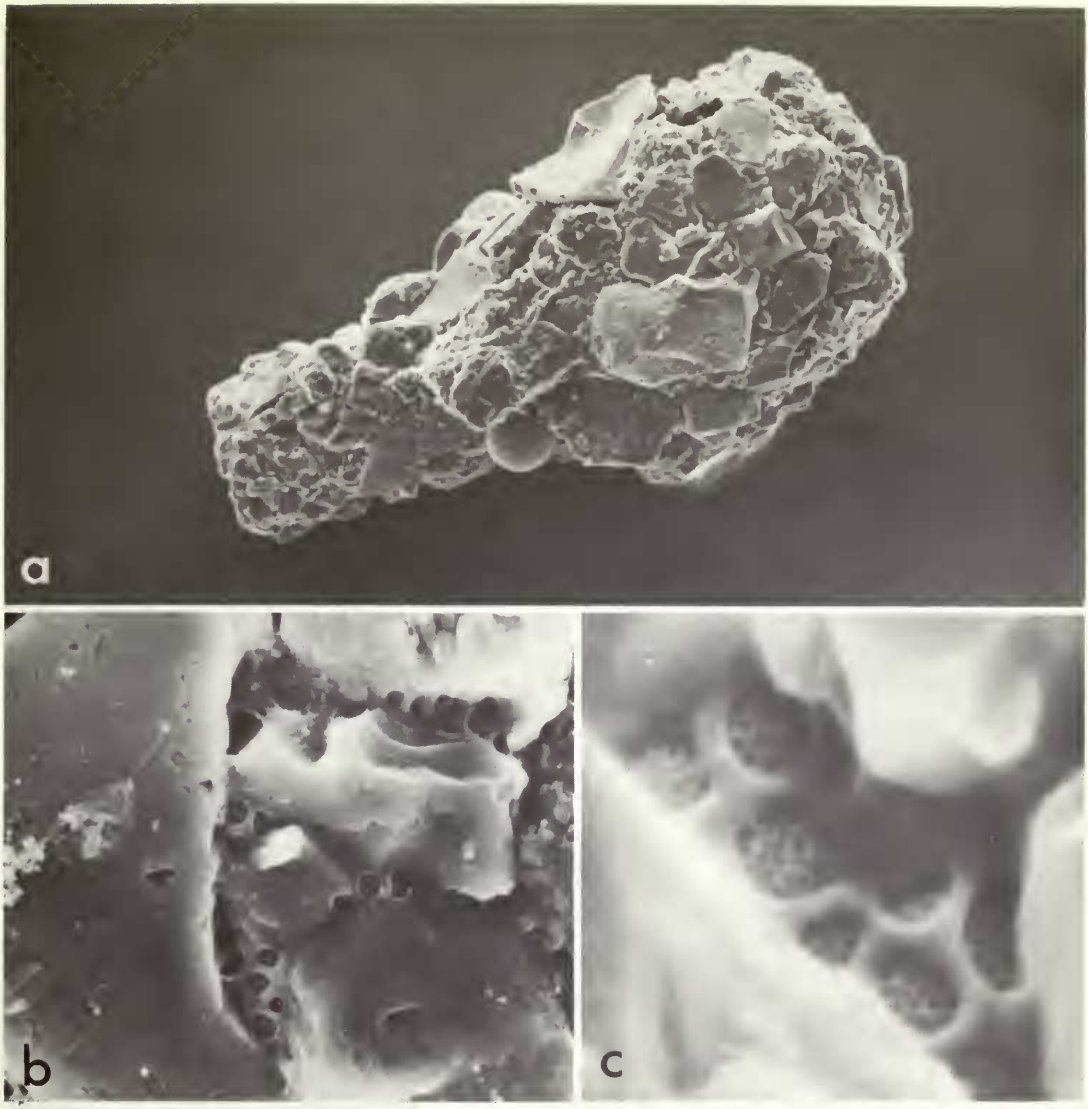

Fig. 3 *Difflugia gassowskii:* a, lateral view ×810; b, shell surface with small areas of organic cement ×7600; c, detail of organic cement network ×24 000.

REMARKS. This species has been redescribed recently (Ogden & Hedley, 1980), but is included here on two counts, the added detail of the organic cement and the change of name. The name *D. longicollis* was used initially by Ehrenberg (1854) to describe specimens which now are not considered to belong to the genus *Difflugia,* nevertheless, under the Rules of Zoological Nomenclature the name is preoccupied. I am grateful to Dr. E. G. Merinfeld, Dalhousie University, Halifax, Nova Scotia, for drawing my attention to this point.

ENTYMOLOGY. This species is named after Dr G. N. Gassowsky who first described it from the Karéliens Lakes.

Difflugia glans Penard, 1902

DESCRIPTION. The shell is dark, elongate ovoid, tapering towards the aperture and evenly rounded aborally (Fig. 4a). It is composed mainly of small to medium pieces of quartz,

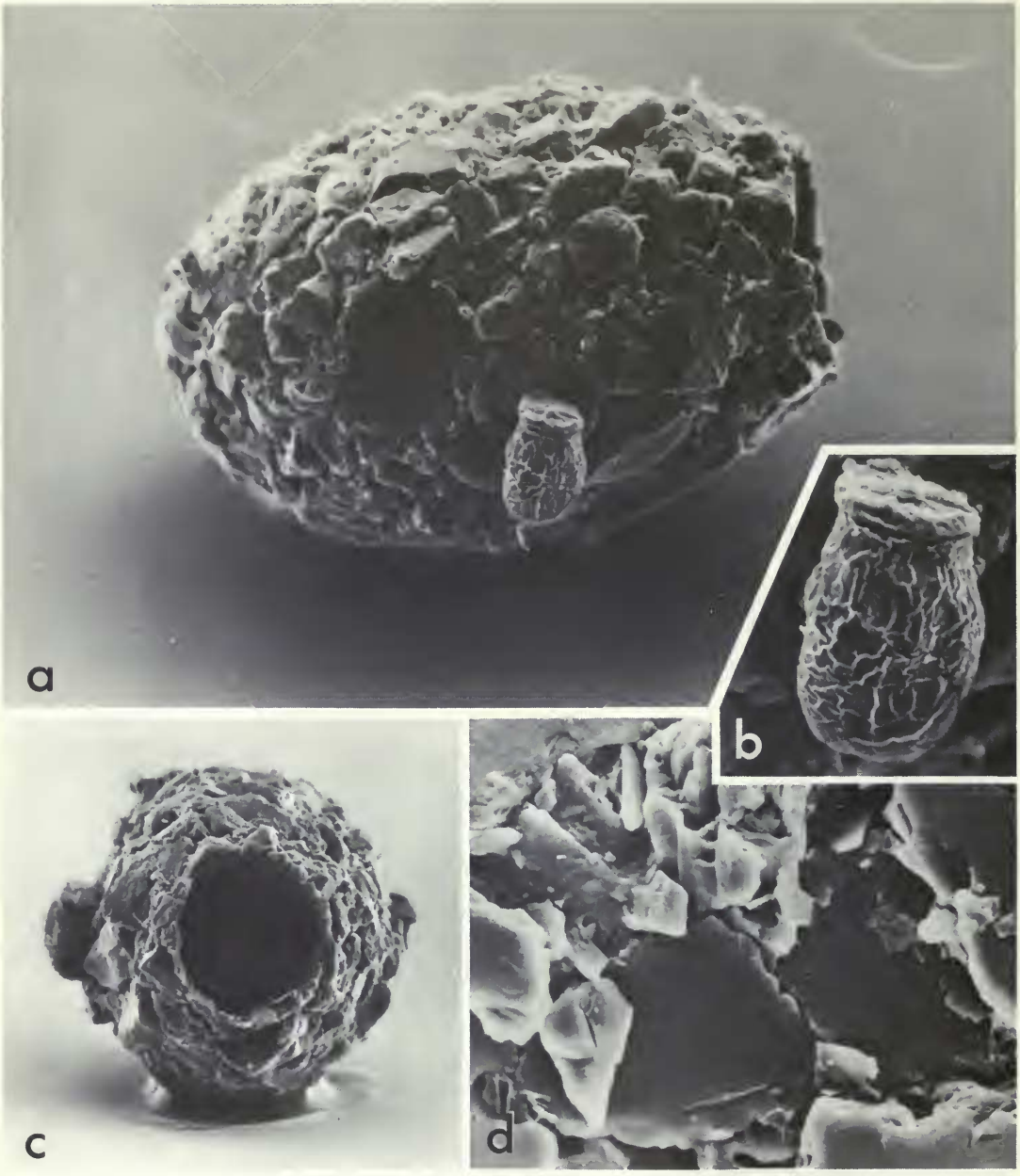

Fig. 4 *Difflugia glans:* a, lateral view ×1400; b, detail of small unidentified cyst ×3000; c, apertural view ×1000; d, portion of shell surface showing the close packing of particles ×3500.

packed closely together with only a minimum amount of organic cement visible (Fig. 4d). A small cyst, of unknown origin, is seen adhering to the surface of the illustrated specimen (Fig. 4b), otherwise the outline is usually well defined. The aperture is circular and surrounded by both small and medium particles (Fig. 4c).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from a sample of water plants taken at the

banks of the River Brett, near Hadleigh, Suffolk in August, 1979 and a gathering of *Sphagnum* moss from Mynnd Hiraethog, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Austria (Laminger, 1973*b*), Congo (Chardez, 1964), Czechoslovakia (Rosa & Lhotsky, 1971; Štěpánek, 1952), Germany (Jung, 1936; Schönborn, 1962), Italy (Grandori & Grandori, 1934; Rampi, 1950), Russia (Kourov, 1925).

REMARKS. This species has not been widely reported, which may be because it falls within the range of three more common species namely, *D. penardi, D. manicata* and *D. rubescens.* It differs from these three species in being a distinct ovoid shape, from *D. rubescens* in being dark and not transparent—although Penard's description of a thin, fragile shell for *D. glans* does not seem compatible with a dark structure which usually suggests that it is robust and strong—and from *D. penardi* and *D. manicata* in aperture size and shape.

Difflugia lacustris (Penard, 1899) comb. nov.

Difflugia pyriformis var. *lacustris* Penard, 1899
Difflugia oblonga var. *lacustris* Cash & Hopkinson, 1909

DESCRIPTION. The shell is transparent or hyaline, elongate, cylindrical or slightly pyriform (Figs. 5a & b). It is composed of small to medium pieces of quartz, diatom frustules and small siliceous flagellate cysts blended together to form a thin structure intermediate between smooth and rough. Only small areas of organic cement occur at the junction of the shell components (Fig. 5d). The cement is in the form of thick-walled rings, between 700–800 nm in diameter, perforated with either three or four holes, 120–160 nm in diameter, which gives these units a similar shape to a button (Fig. 5e). The cement may occasionally be seen either as rings with a slight indentation or as a network of joined rings. When organised as a network the walls of individual rings may be fused together but the typical button-like form are usually seen at the edges. The aperture is usually circular and surrounded by small particles so that the margin is smooth (Fig. 5c).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from three samples in the same locality, aquatic plants at the edge of a pond in Burley, and two gatherings of *Sphagnum* from opposite banks of a small stream at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Dioni, 1970; Lena & Zaidenwerg, 1975), Austria (Laminger, 1973*b* 1974, 1975), Belgium (Chardez, 1980; Chardez & Gaspar, 1976; Oye, 1953), British Isles (Cash & Hopkinson, 1909), Congo (Chardez, 1964; Gauthier-Lièvre & Thomas, 1958), Czechoslovakia (Štěpánek, 1967), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Jung, 1936; Schönborn, 1962*a* & *b*), Guatemala (Laminger, 1973*a*), Italy (Rampi, 1950), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Mexico (Laminger, 1973*a*), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Moraczewski, 1961, 1965), Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Switzerland (Penard, 1902), United States of America (Laminger *et al.*, 1979; Wailes, 1912).

REMARKS. The specimens described here agree well with the original description (Penard, 1899)—shell long, cylindrical, larger in the rear, rarely with a small constriction of the neck—and those given later by Penard (1902) and Cash & Hopkinson (1909). Nevertheless, it would appear that these earlier descriptions were based on groups of similar specimens, hence Penard's reference to a constriction of the neck and the diverse illustrations provided by Cash & Hopkinson. As a result of the latter diagrams, two specimens were tentatively identified as *D. lacustris* in a previous publication (Ogden, 1980). Additional specimens to

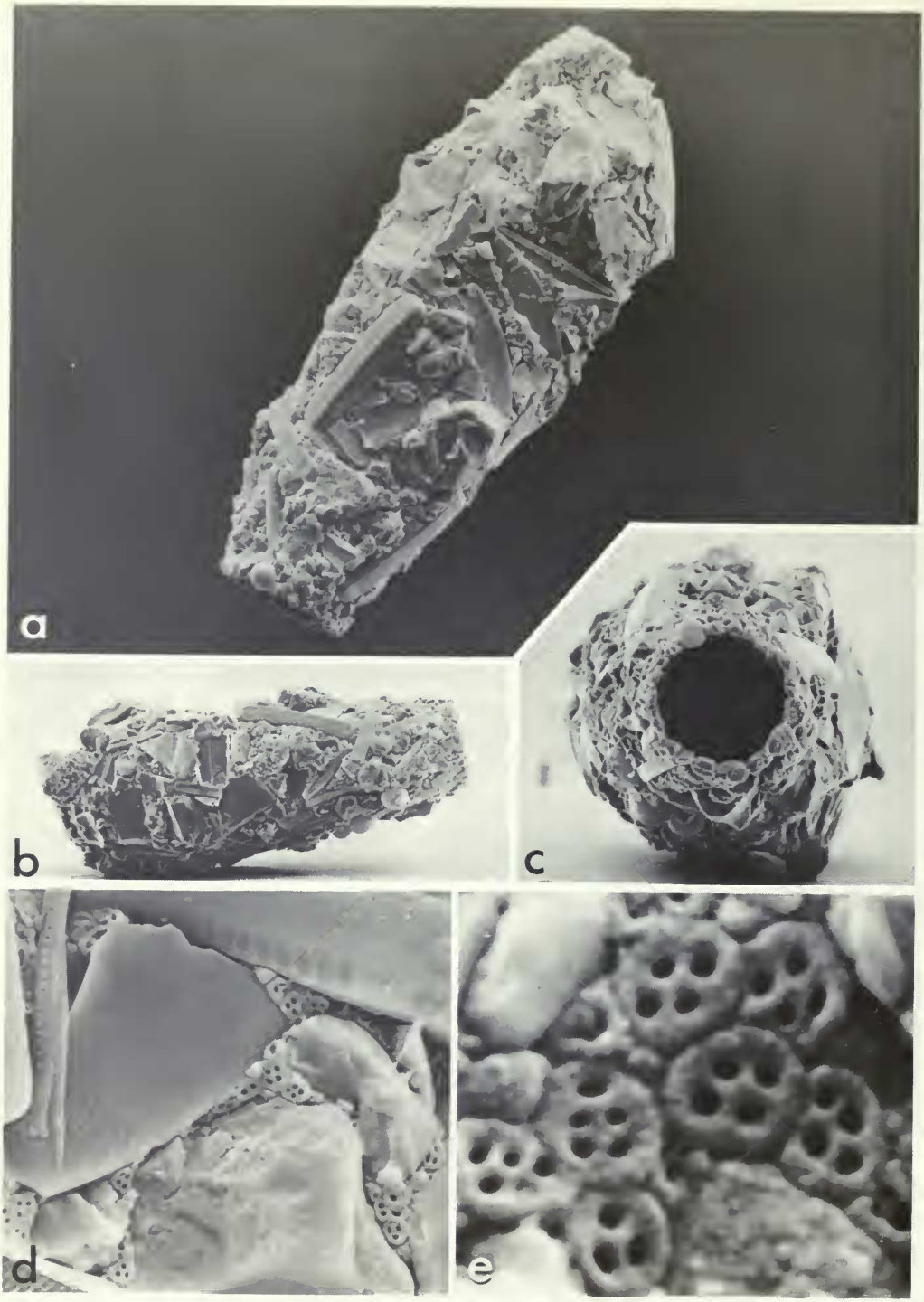

Fig. 5 *Difflugia lacustris:* a, lateral view ×450; b, alternative view of same specimen (a.) to illustrate the uniform shape ×280; c, apertural view ×500; d, shell surface showing the distribution of organic cement ×5800; e, detail of organic cement network ×24 000.

the two mentioned above have been examined and are clearly seen to differ from *D. lacustris*, they are now referred to *D. linearis* (see below).

The present account shows that *D. lacustris* has a well defined shape and a distinctive patterning of organic cement which are considered sufficient to designate this a distinct species.

Difflugia lanceolata Penard, 1890

DESCRIPTION. The shell is yellow or hyaline, lanceolate, tapering from the widest diameter situated about two-thirds of the body-length from the aperture, to give a clean outline that is rounded aborally and evenly angled towards the aperture (Fig. 6a). It is composed of small to medium flattish pieces of quartz and some flat diatom frustules so arranged that the shell is thin and smooth, the surface frequently appearing as though it had been polished, a feature that often permits easy identification. An angular piece of quartz may occasionally protrude from the surface but these are uncommon and limited to one or two in any one shell. As the shell components are usually arranged so that they are in close contact with each other there are no large areas of organic cement, nevertheless, a network of small rings of organic cement may be seen between these particles (Figs. 6d, e, f). The rings are 240–300 nm in diameter and have a distinct wall about 150–200 nm in thickness with a smooth membrane over the mesh. When several rings fuse to form a sheet the thick wall is still usually apparent. The aperture is circular and well defined because the rim has a thin covering of organic cement (Figs. 6b & c).

Variation appears to be limited to cigar-shaped specimens which have almost parallel sides, one such specimen is illustrated by Ogden & Hedley (1980).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. The majority of specimens came from a sample of *Sphagnum* moss collected close to a small stream at Holmsley Lodge, Burley, New Forest, Hampshire, a few came from a similar sample on the opposite bank where they were equally abundant, both samples were taken in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Argentina (Vucetich, 1973*a, b*), Austria (Laminger, 1972*c*), Belgium (Chardez, 1961; Oye, 1953), Brazil (Green, 1975), British Isles (Cash & Hopkinson, 1909; Ogden & Hedley, 1980), Canada (Decloitre, 1965), China (Decloitre, 1965), Congo (Chardez, 1964), Czechoslovakia (Opravilová, 1974), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Schönborn, 1975), Hungary (Gal, 1969), Java (Bartoš, 1963*a*), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970; Moraczewski, 1961, 1965), Roumania (Godeanu *et al.,* 1973), Sudan (Gauthier-Lièvre & Thomas, 1958), Switzerland (Penard, 1902), Venezuela (Grospietsch, 1975), West Africa (Decloitre, 1965), United States of America (Decloitre, 1965).

REMARKS. The organic rim surrounding the aperture is shared with one other pyriform species of *Difflugia,* namely *D. rubescens* where the cement is in the form of tooth-like projections (see Pl.66 *in* Ogden & Hedley, 1980). The only other species of which we are aware that has an organic rim is *D. oviformis,* but this was transferred to a new genus *Netzelia* by Ogden, 1979. *D. lanceolata* is characterized by its uniform size and outline.

Difflugia linearis (Penard, 1890) Gauthier-Lièvre & Thomas, 1958

Difflugia oblonga var. *linearis* Penard, 1890
Difflugia lacustris in Ogden, 1980

DESCRIPTION. The shell is transparent, flask-shaped or elongate pyriform, having a long thin neck with parallel sides and a slightly swollen, rounded aboral region (Fig. 7a). The surface is sometimes slightly uneven because of projecting particles, but generally it has a regular

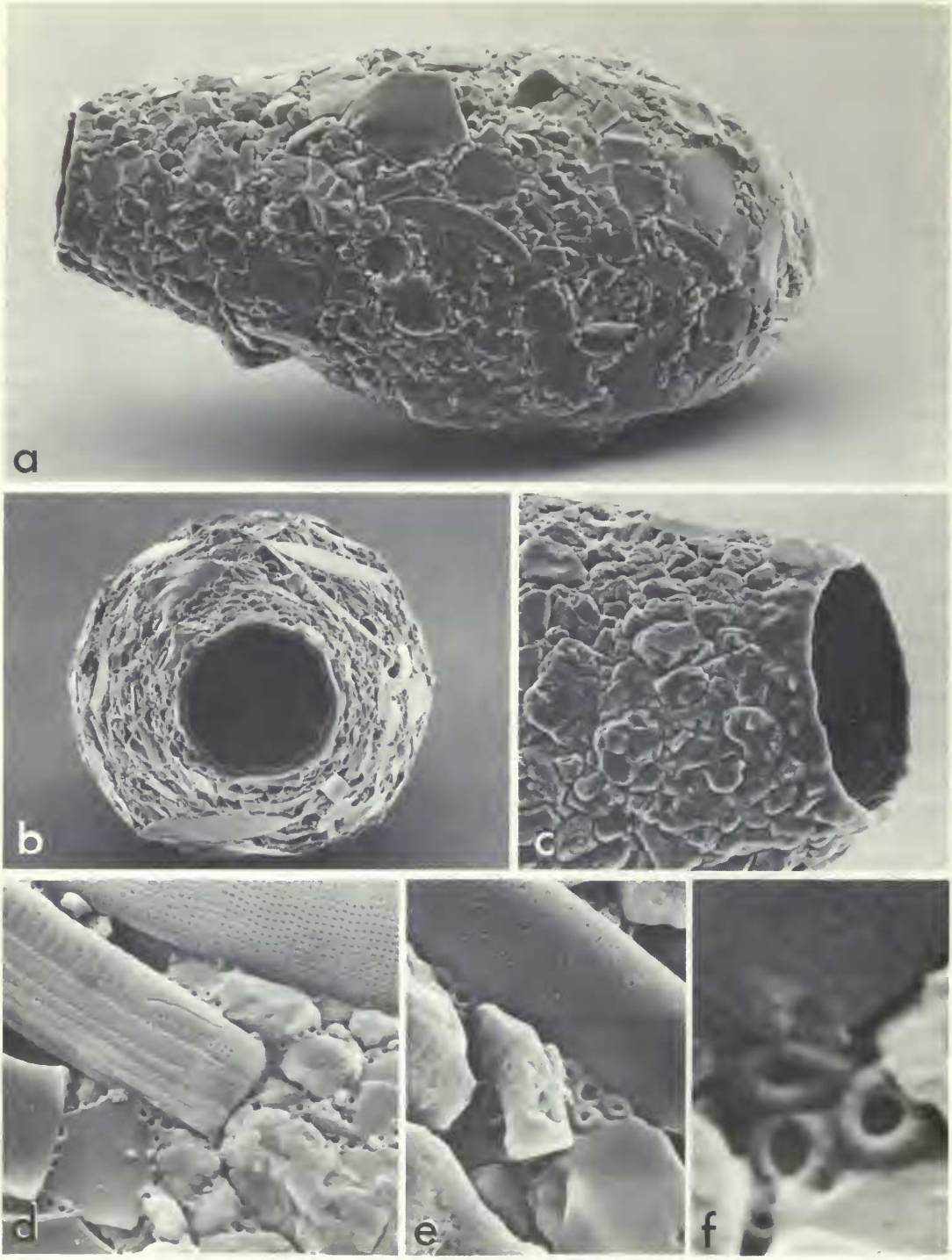

Fig. 6 *Difflugia lanceolata:* a, lateral view ×930; b, apertural view ×760; c, side view of aperture to illustrate the thin covering of organic cement around the rim ×1500; d, shell surface with small isolates of organic cement ×4400; e, small rings of organic cement between particles ×7600; f, detail of organic cement ×24 000.

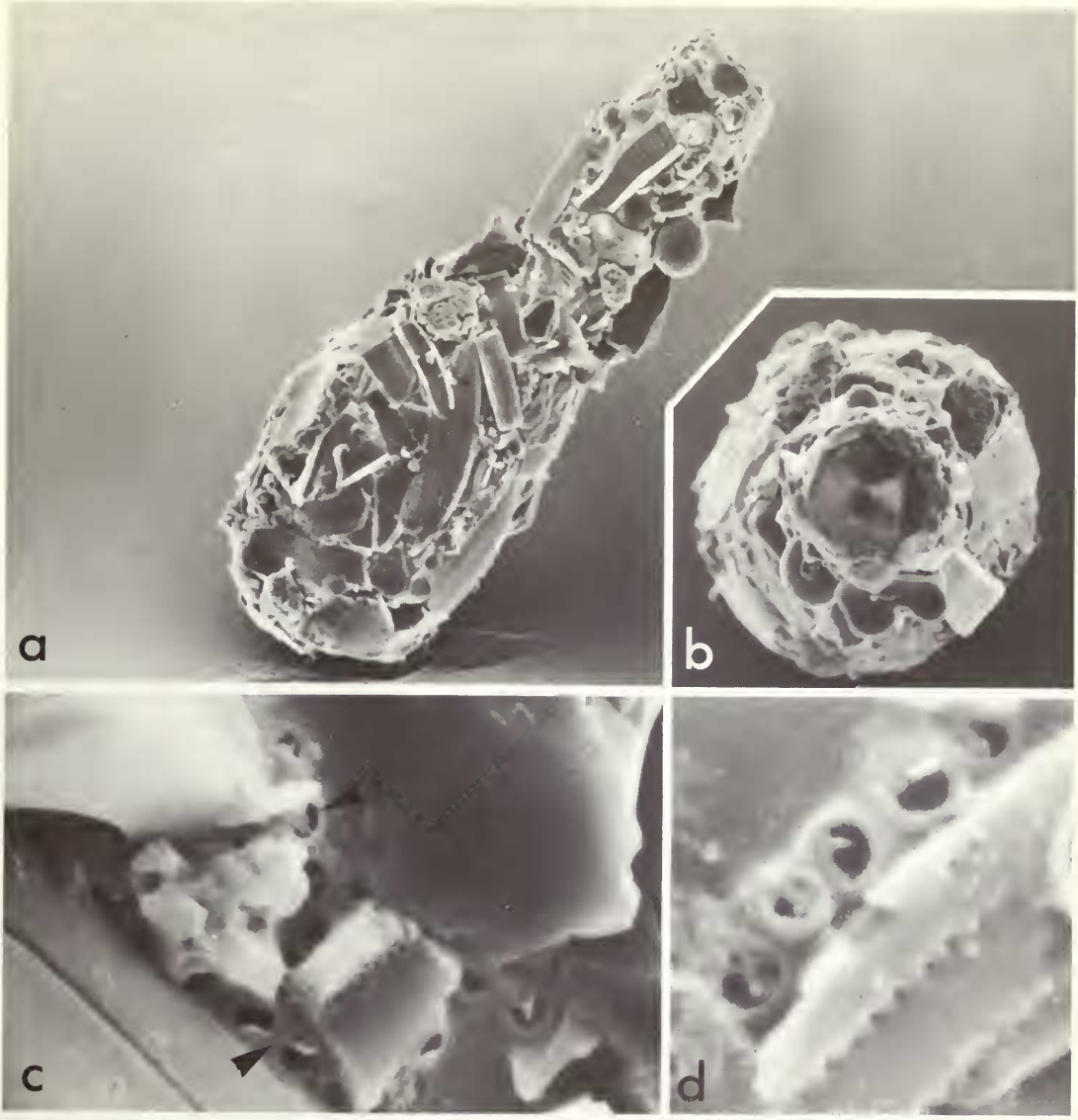

Fig. 7 *Difflugia linearis:* a, lateral view ×950; b, apertural view ×1200; c, portion of shell surface showing areas of organic cement (arrowed) ×14 000; d, detail of organic cement ×24 000.

outline. It is composed of a mixture of flattened pieces of quartz, small whole, flat diatom frustules, fragments of flattish frustules, small siliceous shell plates and round flagellate cysts. Small areas of organic cement, in the form of a network with an open mesh, are occasionally seen (Fig. 7c), The open mesh has a diameter of about 300 nm and walls 100 nm thick (Fig. 7d). In appearance, the openings of the mesh suggest that it may have been covered at some time and has subsequently been broken, but only the examination of further specimens will establish its normal condition. The aperture is circular and usually surrounded by small particles (Fig. 7b).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at Holmsley

Lodge, Burley, New Forest, Hampshire on two occasions, May, 1978 and March, 1980, and at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Austria (Laminger, 1973*b*, 1975), Belgium (Chardez, 1961*b*), British Isles (Ogden, 1980), Bulgaria (Golemansky, 1967), Congo (Chardez, 1964), France (Thomas, 1954), Germany (Penard, 1890), Ivory Coast (Gauthier-Liévre & Thomas, 1958), Nepal (Laminger, 1972*b*), Roumania (Godeanu *et al.*, 1973).

REMARKS. The initial description of this species (Penard, 1890) was brief, and relies mainly on the diagrams. The scarcity of subsequent reports may be due to this inadequate description or the difficulty in finding this species, which by being thin, long and transparent

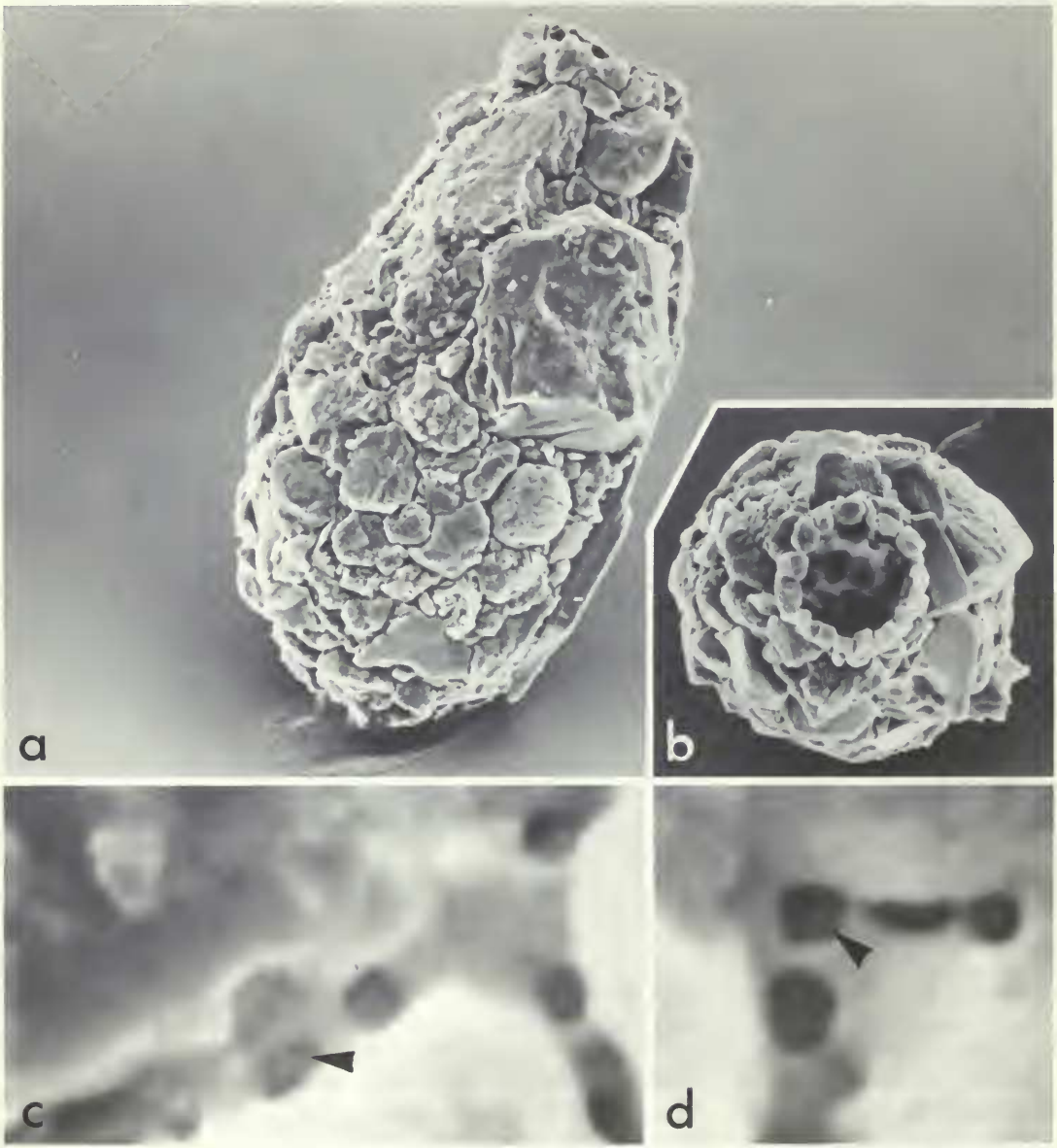

Fig. 8 *Difflugia manicata:* a, lateral view ×1300; b, apertural view ×1100; c, and d, detail of organic cement with the ill-defined inner structure (arrowed) ×30 000.

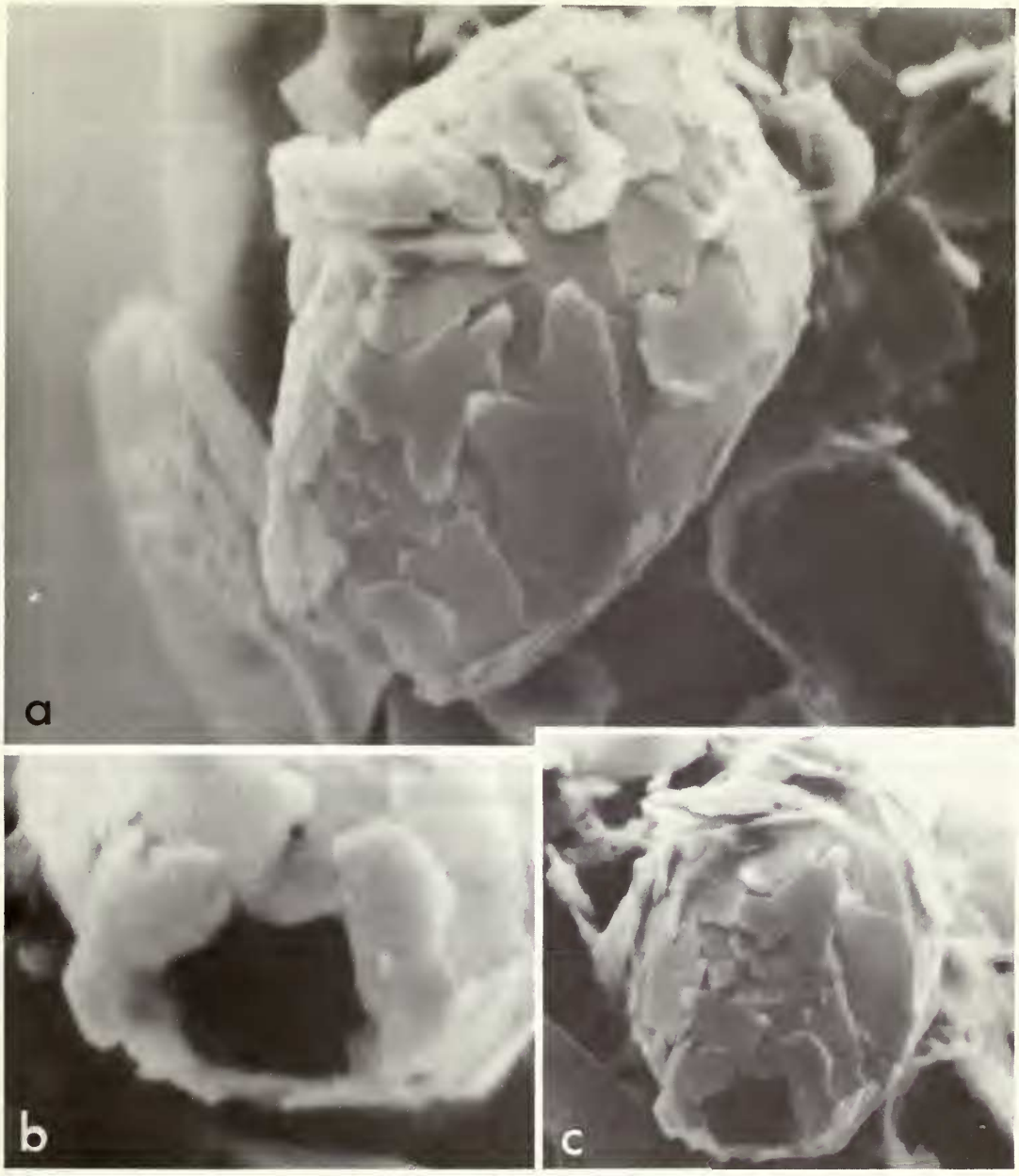

Fig. 9 *Difflugia minutissima:* a, lateral view to show the arrangement of flattish particles ×6700; b, detail of aperture ×10 000; c, latero-apertural view ×4900.

makes it unusually elusive. Two specimens described earlier (Ogden, 1980) and tentatively identified as *Difflugia lacustris,* because of their similarity to the description given by Cash & Hopkinson (1909) and especially to one figure (Pl. XIX Fig. 1), are now redescribed as *D. linearis*. Additional specimens, plus the benefit of being able to compare these with specimens of *D. lacustris* (see p. 9), allows the former identification to be rectified and show that *D. linearis* is a distinct species.

Difflugia linearis can be differentiated from other pyriform species by its distinctive flask-like shape, thin, transparent shell and small aperture.

Difflugia manicata Penard, 1902

DESCRIPTION. The shell is yellow or brown, pyriform, tapering evenly and gradually from a rounded aboral extremity towards the aperture (Fig. 8a). The surface is rough and composed mainly of small to medium pieces of quartz, although the occasional specimen may have large particles added. Small areas of organic cement are seen infrequently, due to the close packing of the shell material, but when present they appear either as strands or as pores in a matrix (Fig. 8c). These pores are about 300 nm in diameter and have an ill-defined inner structure which appears to have smaller pores about 130 nm in diameter (Figs. 8c & d). The aperture is circular and surrounded by a distinct pattern of small particles (Fig. 8b).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from samples taken at three sites, *Sphagnum* moss gatherings at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Clwyd, North Wales in August, 1980, and from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Austria (Laminger, 1971, 1972*c*), Belgium (Chardez, 1961*b*), British Isles (Cash *et al.*, 1919; Ogden & Hedley, 1980), Congo (Štěpánek, 1963), Italy (Grandori & Grandori, 1934), Poland (Moraczewski, 1965; Pateff, 1926, 1927), Switzerland (Penard, 1902).

REMARKS. Although this species was thought to be uncommon by Cash, Wailes & Hopkinson (1919), it is suggested that this has been one of the overlooked species and that it will probably be found as one of the most commonly distributed. The wide range of habitat already reported, lake, river and *Sphagnum* moss would appear to support this opinion.

Difflugia minutissima Penard, 1904

Sexangularia minutissima (Penard, 1904) Deflandre, 1931

DESCRIPTION. The shell is transparent, elongate or ovoid, rounded aborally and tapering slightly towards the aperture (Figs. 9a & c). It is composed of thin flattish pieces of quartz, and the occasional diatom frustule, which are arranged so that they overlap, but the result is still a fragile structure. Only small strands of organic cement have been seen at some junctions. The aperature is basically circular, any variation is usually due to the irregular arrangement of particles around the opening (Fig. 9b).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIALS EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Mynnd Hiraethog, Clwyd, North Wales in August 1980.

GEOGRAPHICAL DISTRIBUTION: Switzerland (Penard, 1904)

REMARKS. This species appears to be known only from the initial description (Penard, 1904), although Deflandre (1931) using Penard's description suggested that it should be transferred to the genus *Sexangularia* Awerintzew, 1906. The main features of this latter genus are 'chitinous shell, with or without the addition of extraneous particles; polygonal in transverse section, most often hexagonal'. At present it is considered that these features are insufficient to differentiate this genus from *Difflugia,* and therefore refer the included species to *Difflugia–D. minutissima* Penard, 1904; *D. parvula* (Awerintzew, 1906) and *D. polydera* Deflandre, 1931.

The specimens described here were found adhering to extraneous particles when prepared by air-drying and because of this it is not possible to examine them in transverse section,

nevertheless, they do not appear to be polygonal. The value of this feature in relation to a fragile shell is questionable, especially as Penard's observations would have been carried out on specimens under a cover slip, which would allow a degree of compression. The specimens share similar dimensions to those given by Penard for *D. minutissima* and are so designated.

Difflugia parva (Thomas, 1954) comb. nov.

Difflugia oblonga var. *parva* Thomas, 1954

DESCRIPTION. The shell is pyriform, tapering evenly from the swollen and rounded aboral third, to the aperture for the remaining two-thirds (Fig. 10a). It is composed mainly of a mixture of small to medium pieces of quartz, often with the addition of two or three large pieces. Organic cement is seen between particles usually as a series of single units (Fig. 10c), which may overlap but are seldom fused to form a network. Each unit is a ring about 650–750 nm in external diameter, 300–380 nm internal diameter, with walls about 150 nm thick. A small mesh covers the inner portion of each ring (Fig. 10d). The aperture is circular and surrounded mainly by small particles (Fig. 10b).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at Matley Bog, Lyndhurst, New Forest, Hampshire in March, 1980; Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980 and aquatic plants from a pond at Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Lena & Zaidenwerg, 1975), Austria (Laminger, 1973*b*), Belgium (Chardez, 1980; Chardez & Gaspar, 1976; Couteaux, 1969), Bulgaria (Golemansky, 1967), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Schönborn, 1965; Voeltz–Höhn, 1971), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970; Moraczewski, 1965), Venezuela (Grospietsch, 1975).

REMARKS. There have been several reports of *D. oblonga* var. *parva* since Thomas (1954) described his new variety, although size was the only diagnostic feature used and illustrated (Pl. III, Fig. 1) by him to differentiate this variety from *D. oblonga.* The figure given also shows the difference in shell composition, described below as a specific feature.

This variety is considered as a distinct species from *D. oblonga* because of its clean outline, relatively smooth surface and detailed cement pattern.

Difflugia paulii nom. nov.

Difflugia oblonga var. *elongata* Oye, 1953

DESCRIPTION. The shell is transparent, slim and elongate, tapering evenly from just anterior of the mid-body region towards the aperture, the even-tapering is more apparent in Fig. 11b whereas the upper side of Fig. 11a has a misleading hump, the posterior region is slightly swollen, curving sharply and smoothly at the extremity (Fig. 11a). It is composed of flattish pieces of quartz to give a smooth appearance, with small areas of organic cement often apparent as part of the matrix (Fig. 11c). The cement is in the form of small perforated cones about 600 nm in diameter, the perforations being about 100–150 nm in diameter (Fig. 11d). The aperture is circular and surrounded by small pieces of quartz (Fig. 11b).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

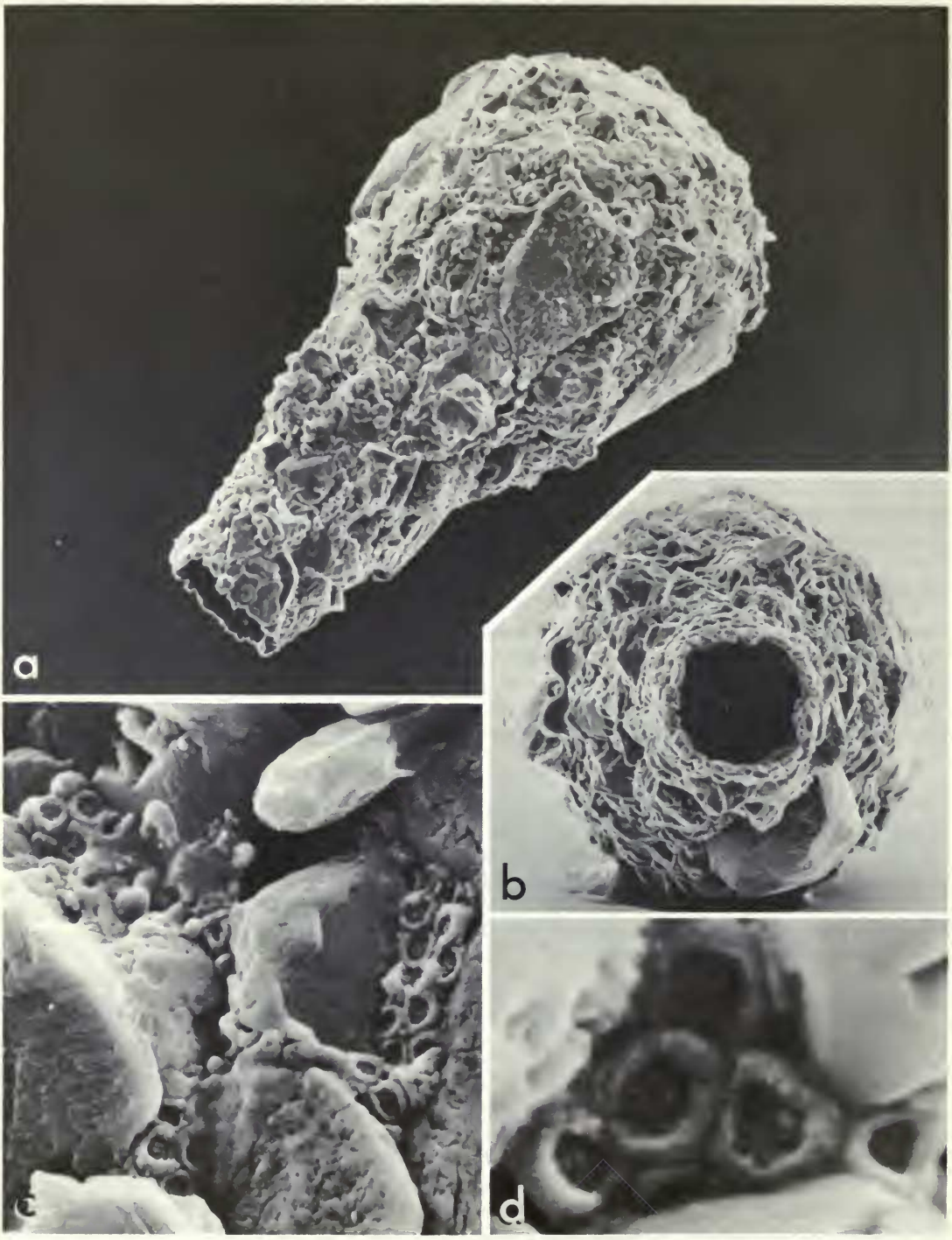

Fig. 10 *Difflugia parva:* a, lateral view ×710; b, apertural view ×790; c, shell surface showing areas of organic cement ×9800; d, detail of organic cement ×30 000.

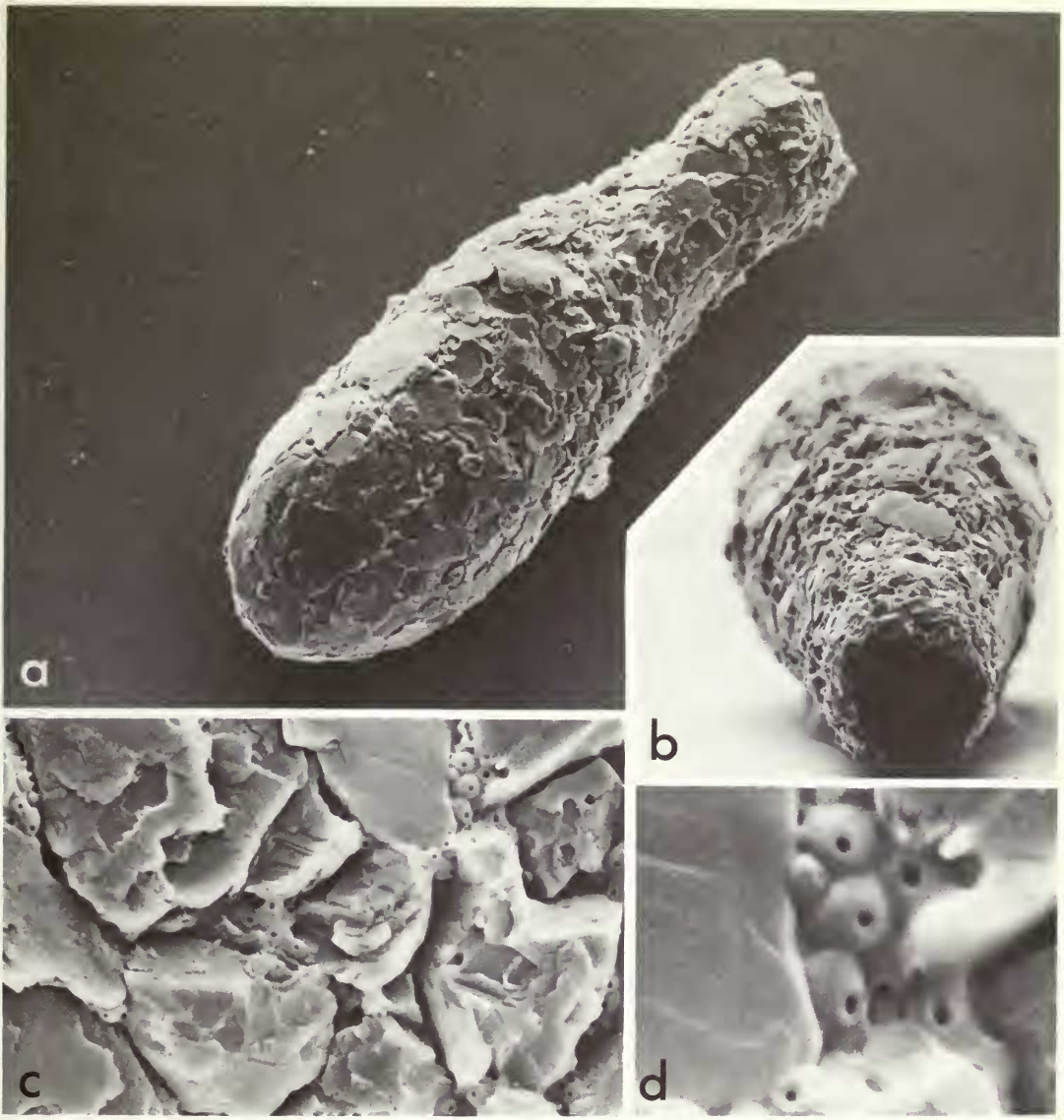

Fig. 11 *Difflugia paulii:* a, lateral view ×800; b, apertural view ×790; c, portion of shell surface ×4600; d, detail of organic cement ×15 000.

GEOGRAPHICAL DISTRIBUTION. Austria (Laminger, 1973*b*), Belgium (Oye, 1953), Congo (Gauthier-Lièvre & Thomas, 1958), Spain (Gracia, 1972*a*).

REMARKS. This species has been described on two occasions, from Belgium by Oye (1953) and from Africa by Gauthier-Lièvre & Thomas (1958). Oye (1953) stated that these specimens were slender in comparison with *D. lacustris,* and considered that this feature and the limited grains of quartz in the shell was sufficient to warrant a new variety. Gauthier-Lièvre and Thomas (1958) agreed with this earlier description and designation.

Of the more elongated pyriform species, *D. paulii* in body length appears to occupy a position mid-way between *D. linearis* and *D. lacustris,* the present work shows that it is distinct from these two species in outline, elemental composition and patterning of the

organic cement, in addition, it can be differentiated from *D. linearis* by the size of the aperture (Table 1).

ETYMOLOGY. This species is named after Dr Paul van Oye whose original description was based on specimens from a pond in Belgium.

Difflugia petricola Cash, 1909

This species has been redescribed recently by Ogden & Fairman (1979). It is reported here only to demonstrate the regularity of dimensions between specimens from different localities, see Tables 1 and 2, because these are often used as taxonomic features.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at two sites, Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

Difflugia pristis Penard, 1902

DESCRIPTION. The shell is brown or opaque, ovoid, tapering from the mid-body position towards the aperture and gracefully curved aborally (Fig. 12a). It is thin, smooth and composed of flattish pieces of quartz (Fig. 12a-c) or infrequently including flat pieces of diatom frustule. The particles are packed closely together and only small connections of organic cement are visible (Figs. 12d & e). The aperture is circular with a regular margin (Fig. 12b).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in May, 1978 and at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. British Isles (Cash & Hopkinson, 1909), Czechoslovakia (Štěpánek, 1967), Hungary (Varga, 1963), Italy (Grandori & Grandori, 1934), Java (Bartoš, 1963*a*), Poland (Moraczewski, 1965), Roumania (Godeanu *et al.*, 1973), Switzerland (Penard, 1902).

REMARKS. Cash and Hopkinson (1909) considered their specimens to be in good agreement with Penard's (1902) description, except for the absence of refractive particles that made the shell appear opaque or black. This they attributed to the difference in habitat of their samples, the former being found amongst floating vegetation in clear water and Penard's from a muddy lake bottom. Some differences in size have been reported since Penard who gave 45–65 μm as the range of length, Cash and Hopkinson gave 60–65 μm, whilst more recently Varga (1963) found specimens measuring 44–48 μm in length.

The specimens reported here are smaller than any previously described, although in all other respects agree with Penard's description. The main features that distinguish *D. pristis* from *D. pulex* are the darker colour and the more regular shape.

A single larger specimen, 56 μm long, 31μm wide, aperture 10 μm in diameter, with the typical pyriform shape (Fig. 13a & b) was found in the sample from Wales. This is reported here as being questionably *D. pristis* (?), being atypical in having a definite neck, the discovery of more specimens may result in a more accurate identification. This specimen is similar to those identified by Cash & Hopkinson (1909) as (?) *D. pulex* which they described as being 'oval, tapering suddenly to a short neck'.

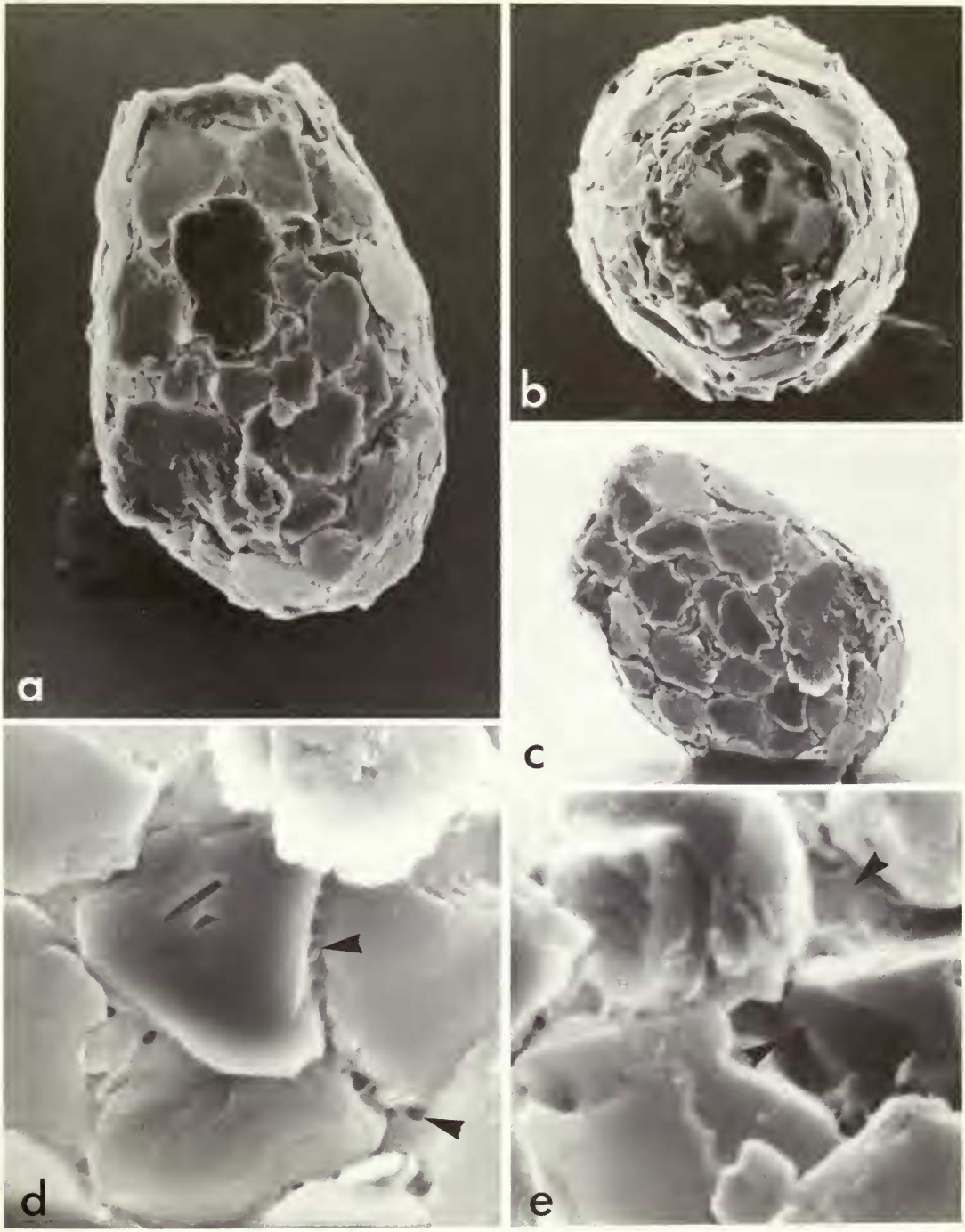

Fig. 12 *Difflugia pristis:* a, lateral view ×2400; b, apertural view ×2400; c, alternative view of specimen shown in a., to illustrate regular ovoid shape ×1700; d and e, portions of shell surface with small connections of organic cement (arrowed) ×9300 and ×14,000.

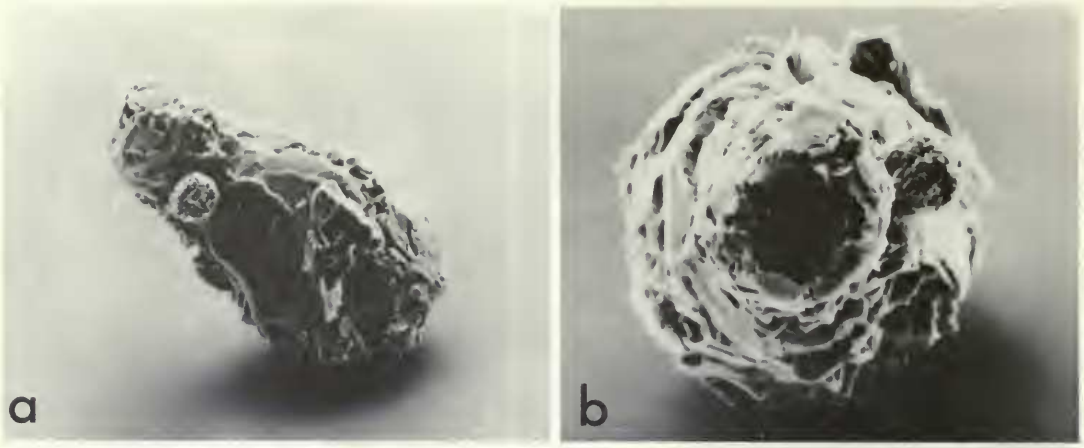

Fig. 13 *Difflugia pristis* (?): a, lateral view to show distinct neck ×860; b, apertural view ×1600.

Difflugia pulex Penard, 1902

Difflugia minuta minor Godeanu, 1972

DESCRIPTION. The shell is transparent, elongate or ovoid (Figs. 14a & d). It is composed mainly of a mixture of small thin pieces of flat quartz and pieces of diatom frustule, often with whole frustules or round flagellate cysts adhering to the surface (Figs. 14a–e). The arrangement of these particles is such that only small strands of organic cement are visible. The aperture is usually circular (Fig. 14c) but may vary due to the arrangement of the surrounding particles (Fig. 14b).

MEASUREMENTS (in μm). See Tables 1 & 2.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Subberthwaite, Broughton in Furness, Cumbria in June 1979 and at Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Argentina (Lena & Zaidenwerg, 1975), Australia (Playfair, 1918), Austria (Laminger, 1973*b*), Belgium (Chardez, 1961*b*), British Isles (Cash & Hopkinson, 1909), Congo (Štěpánek, 1963), Czechoslovakia (Štěpánek, 1967), Germany (Schönborn, 1962*a* & *b*), Italy (Grandori & Grandori, 1934; Rampi, 1950), Java (Bartoš, 1963*a*), Netherlands (Hoogenraad & Groot, 1940), Roumania (Godeanu *et al.*, 1972), Spain (Gracia, 1972*b*), United States of America (Laminger *et al.*, 1979), West Africa (Decloitre, 1948).

REMARKS. Penard's original description stated that the shell was–' pyriform, with or without narrowing of the mouth, chitinoid, slightly yellow, covered with small scales or particles of amorphous silica, plates, sufficiently transparent to examine the contents' and that specimens rarely exceeded 30 μm in length. Cash & Hopkinson (1909) described specimens between 65–70 μm in length that they tentatively identified as *D. pulex*, but on the basis of both Penard's and the present description it is now suggested they should be reassigned.

The description of *D. minuta minor* given by Godeanu (1972), shell colourless circular in cross section but with an irregular outline because of added quartz particles and a circular aperture, is so similar to that of *D. pulex* that it must be considered a synonym. The range of measurements given are also similar to those quoted here (see Table 1).

Although Penard gave 30 μm as the maximum length for this species, in the described sample two specimens were just in excess of 40 μm and two 30 μm, but in all other respects were similar to the smaller specimens, and all are considered to represent *D. pulex*.

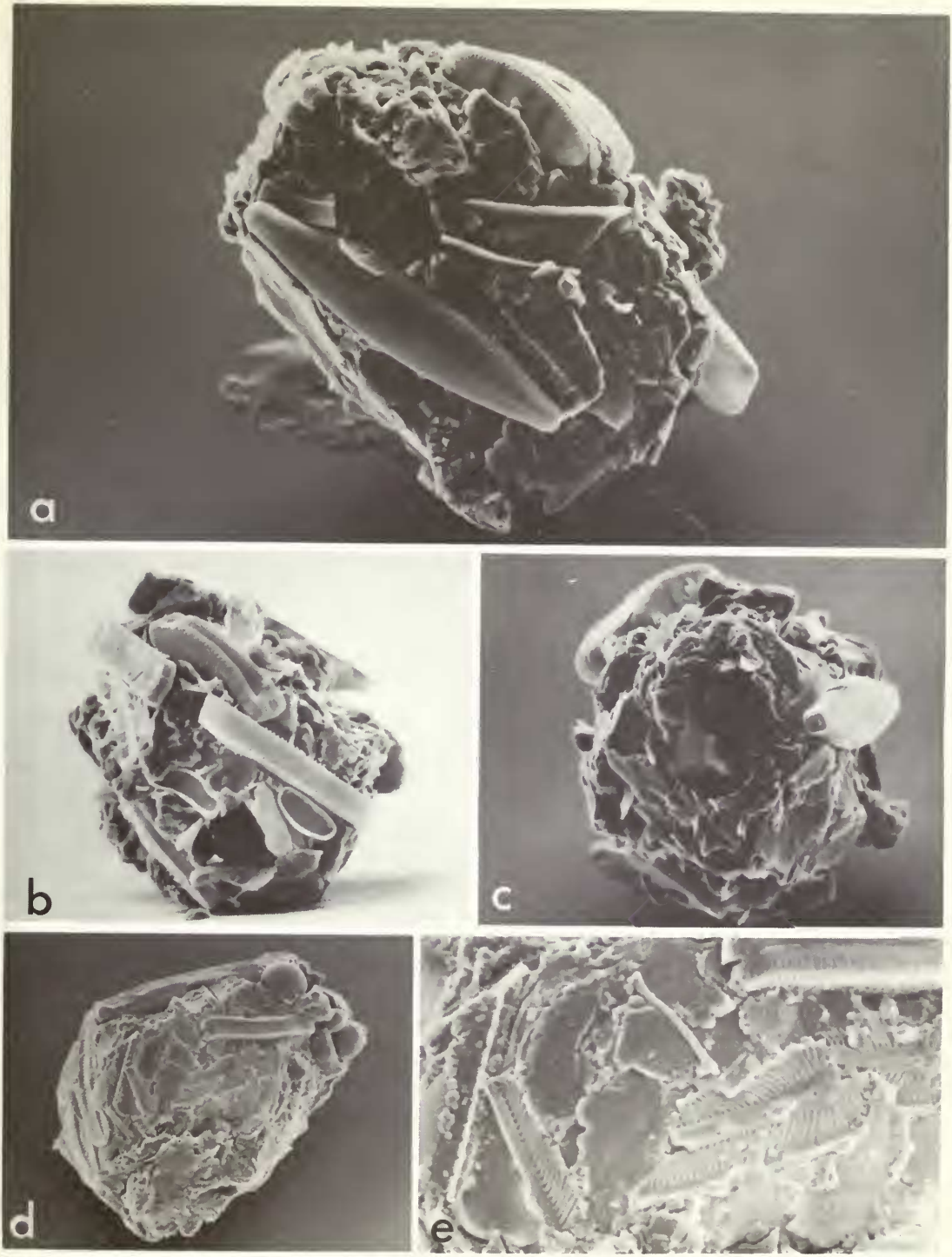

Fig. 14 *Difflugia pulex:* a, lateral view ×1800; b, apertural view of specimen with irregular apertural opening ×1300; c, apertural view of specimen (a.) with circular aperture ×1500; d, lateral view of specimen mainly made of flattish particles ×1600; e, shell surface showing mixture of flat components ×5100.

Difflugia tenuis (Penard, 1890) comb. nov.

Difflugia pyriformis var. *tenuis* Penard, 1890
Difflugia oblonga var. *tenuis* Wailes & Penard, 1911

DESCRIPTION. The shell is usually transparent, cylindrical or slightly pyriform, composed of a mixture of mainly small to medium pieces of angular quartz, but with an occasional large particle added (Figs. 15a & b). Sometimes additional particles give a pointed outline to the aboral region, instead of the usual rounded contours. Organic cement is seen frequently as single units between shell components (Fig. 15d), and occasionally in small patches where these units are in a network with a mesh diameter of 350–400 nm and walls 180–220 nm thick (Fig. 15e). The mesh surface is characterised by a thin, usually central, inner ring about 150–200 nm in diameter (Fig. 15e). The aperture is roughly circular, often having an irregular outline because of the mixture of particles surrounding it (Fig. 15b).

One specimen with projections similar to the rigid 'filament' structures described by Penard (1890), occurred in the present sample (Fig. 15c). These projections usually arise from a common base, on the surface of the quartz particles, and vary in size and number (Fig. 16a). The projections are about 250 nm in diameter and may be up to 7 μm in length, as many as fifteen have been seen sharing a common base (Fig. 16b). On the present evidence they seem to be rosettes of bacterial rods rather than the parasitic organisms suggested by Penard (1890).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION: Argentina (Dioni, 1970), British Isles (Cash *et al.*, 1919), Germany (Penard, 1890), Poland (Golemansky, 1970), Venezuela (Grospietsch, 1975).

REMARKS. Although the specimens described here are a little longer than those reported by Penard (1890) they are otherwise in good agreement with his description. This species has been identified previously on only a few occasions, but this may be due to its being mistaken for the more common species in this size range, for example *D. penardi* and *D. rubescens*. There remains the question of specific biological requirements, food, temperature, pH etc., which may be the reason why although the site at Holmsley has been sampled regularly for five or six years, March 1980 was the first time that this species has been seen there and then it appeared in significant numbers. This species is distinguished by its shape, size of aperture and the pattern of the organic cement.

Difflugia viscidula Penard, 1902

DESCRIPTION. This species has been redescribed recently by Ogden & Hedley (1980) but is reported again with some additional information.

The shell is opaque, pyriform or elongate ovoid, aborally it is usually rounded (Fig. 17a) but may occasionally be pointed. It is composed of a mixture of different sizes of angular quartz, with organic cement seen infrequently as part of the surface matrix. The cement appears as single units squashed together so that they are adjacent or overlap (Fig. 17c). The aperture is circular and usually surrounded by small particles which give it a characteristic well-defined outline (Fig. 17b). The illustrated aperture has a cyst plug, which although broken at one edge has in general a smooth surface, suggesting that it is mainly organic but reinforced by particles of quartz. About 10% of the examined specimens had an apertural cyst plug.

MEASUREMENTS (in μm). See Tables 1 and 2.

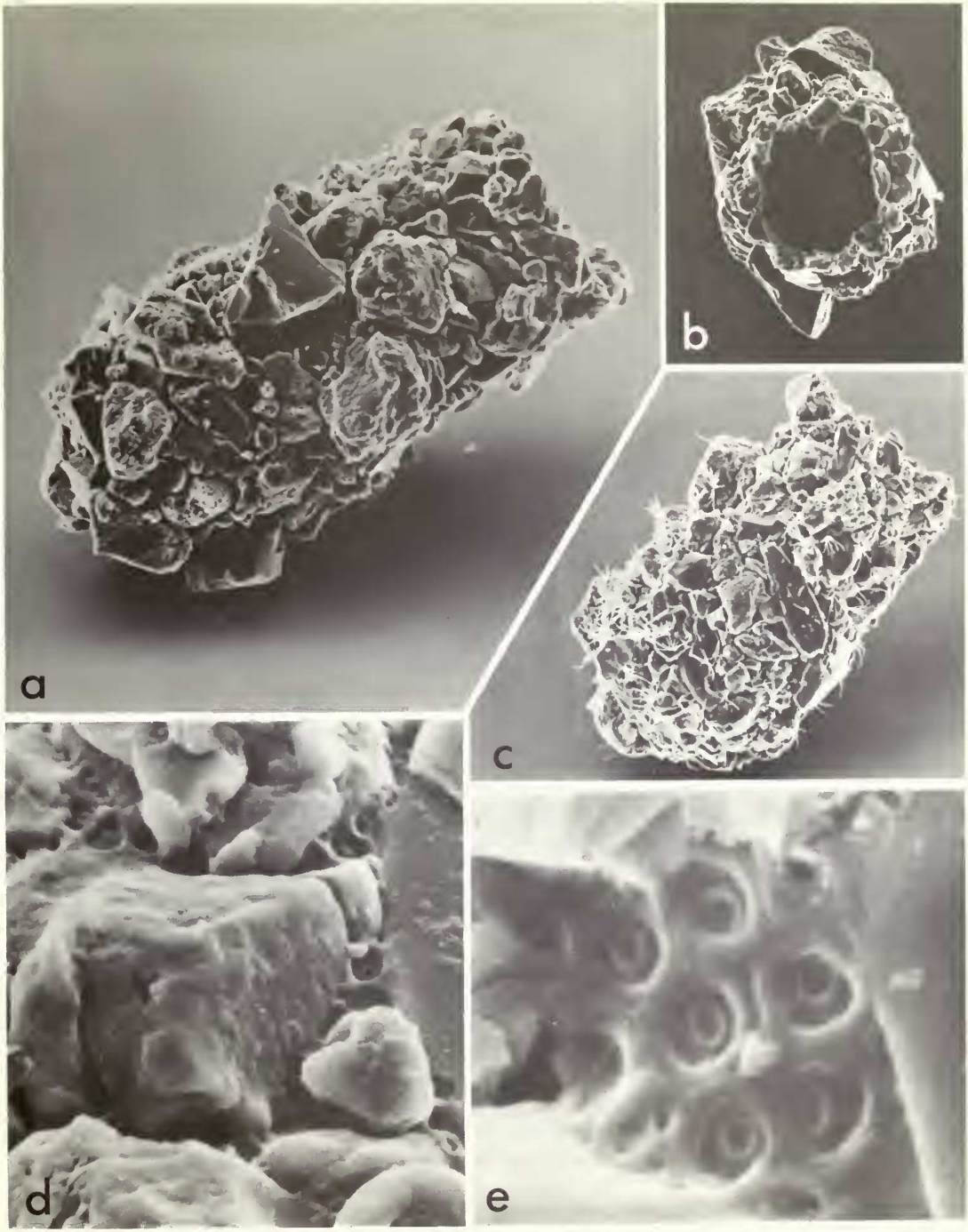

Fig. 15 *Difflugia tenuis:* a, lateral view ×1000, b, apertural view ×780; c, specimen with 'filament-like' structures projecting from the surface ×780; d, shell surface showing small areas of organic cement ×8100; e, detail of organic cement network ×24 000.

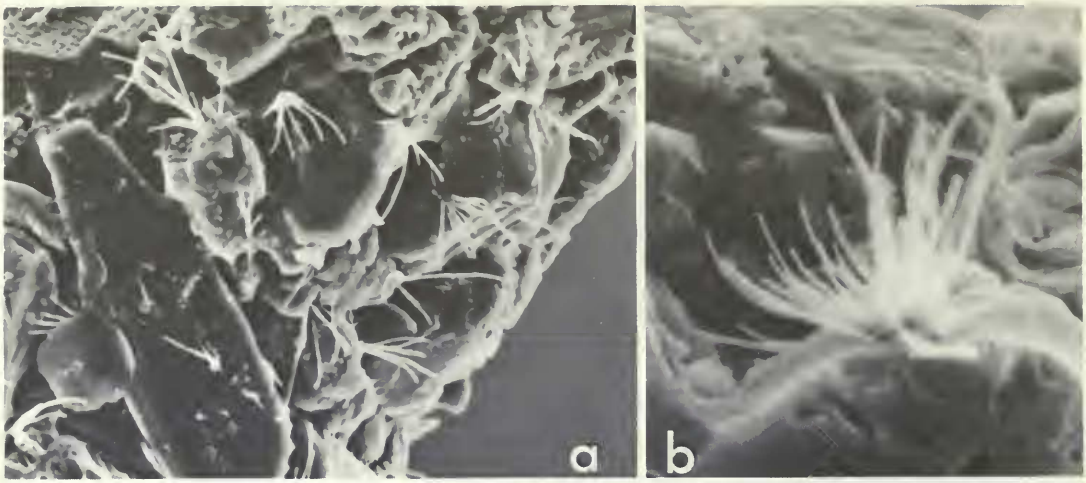

Fig. 16 *Difflugia tenuis:* a, portion of shell surface to show distribution of 'filament-like' structures ×2500; b, rosette of 'filaments', tentatively identified as bacterial rods ×7000.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Argentina (Boltovskoy & Lena, 1974), Austria (Laminger, 1971), British Isles (Ogden & Hedley, 1980), Germany (Schönborn, 1962*a*, 1965, 1975), Java (Bartoš, 1963*a*), Roumania (Godeanu *et al.*, 1973), Switzerland (Penard, 1902).

REMARKS. The present material extends the measurements we gave previously (Ogden & Hedley, 1980) to encompass those given by Penard (1902). There remains the problem of priority of names for these specimens because Penard (1902) described two distinct species, namely *D. lemani* Blanc, 1892 and *D. viscidula* sp. nov., which he differentiated mainly on size; the former being 50–85 μm long (three individuals were 100–200 μm) and the latter 180–260 μm long. When he later found (Penard, 1905) that he had used incorrect measurements for *D. lemani* he suggested that *D. viscidula* should be regarded as a synonym. However, this proposal left his description of specimens under the name *D. lemani*–Penard, 1902 p. 249, without a proper designated name. They were divided into two series, the first slim, between 75–85 μm long and the second wider, but smaller about 50 μm long. It would appear that no subsequent report has rectified this situation, and it would seem that now is too late to change this because of the proliferation of species that have since been described and fall within the size range of the earlier description. Furthermore, it appears that Blanc's (1892) original description of *D. lemanii* might contravene Article 8 of the International Code of Zoological Nomenclature, because when first issued it would seem that it was not available by purchase or free distribution. There are no records of this publication in either this Museum's Libraries nor in the British Library, although I have recently obtained a photocopy from the Universitaire Lausanne. In Blanc's initial description of *D. lemanii* the shell dimensions varied as follows: body length between 180–310 μm, breadth 130–150 μm. and the aperture diameter was given as 110μm, it had a cylindrical body with almost parallel sides and the composition was such that it was friable and delicate. These measurements are in good agreement with Penard's 180–260 μm body length for *D. viscidula,* and those given here in Table 1 except for the diameter of the aperture, this latter feature is given as being equal to about half the breadth of the shell by Penard (1905). The diameter of the aperture and the pyriform rather than cylindrical shape of the body are considered sufficient to differentiate the present specimens and those of Penard (1902, 1905) from *D. lemanii* Blanc, 1892. This therefore leaves Penard's designated name of *D. viscidula* as valid and the specimens described here are so named.

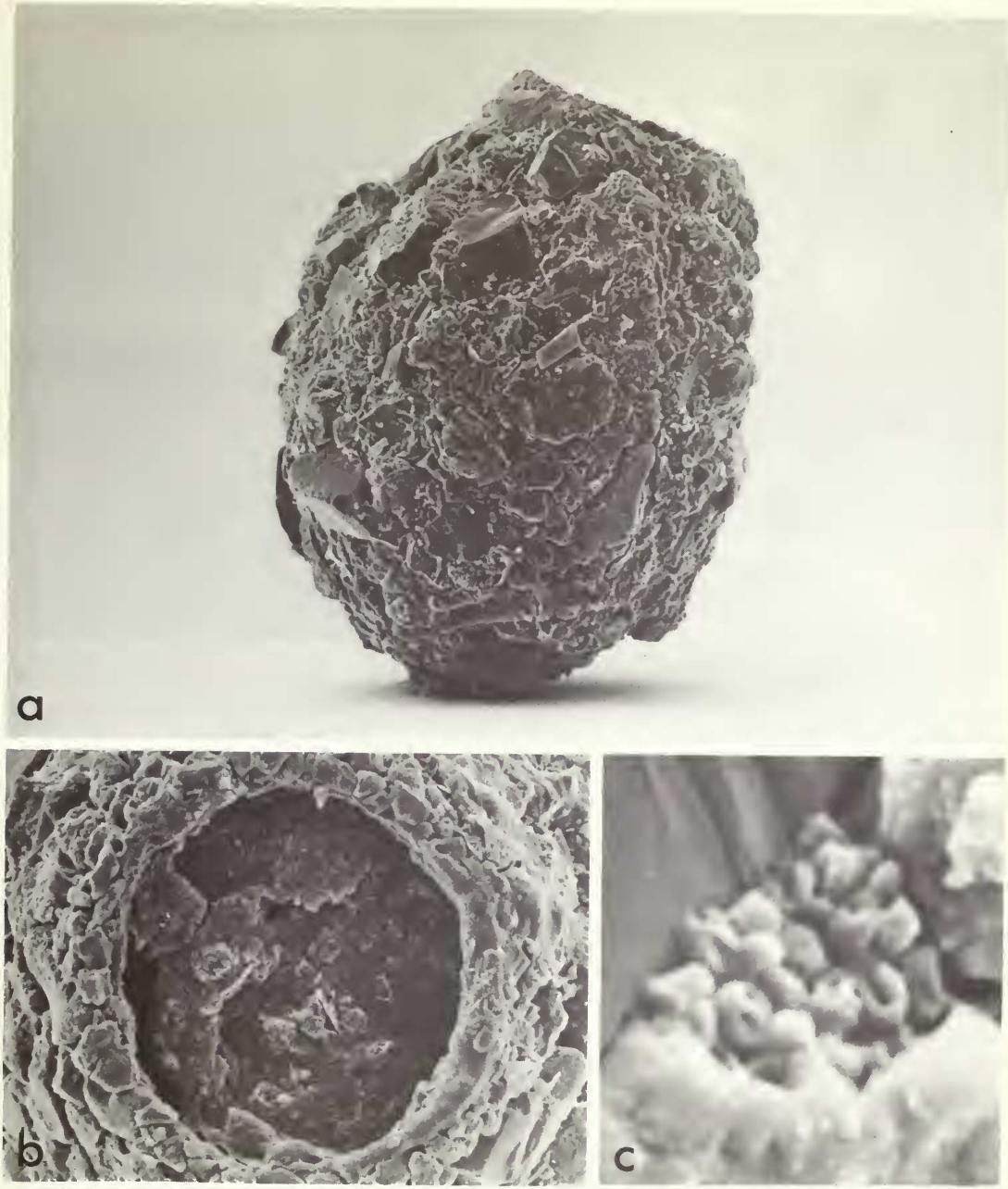

Fig. 17 *Difflugia viscidula:* a, lateral view ×410; b, detail of aperture which is blocked by a cyst plug ×1000; c, detail of organic cement ×13 000.

Pointed species or those with protruberances

Difflugia amphoralis Cash & Hopkinson, 1909

DESCRIPTION. The shell is transparent, squat pyriform with the aboral extremity tapering evenly to a point (Figs. 19a & b). It is composed mainly of medium pieces of quartz with small pieces mixed and so arranged to produce an intermediate smooth surface. Organic cement is seen in small patches between particles (Fig. 19d) and appears as rings fused to

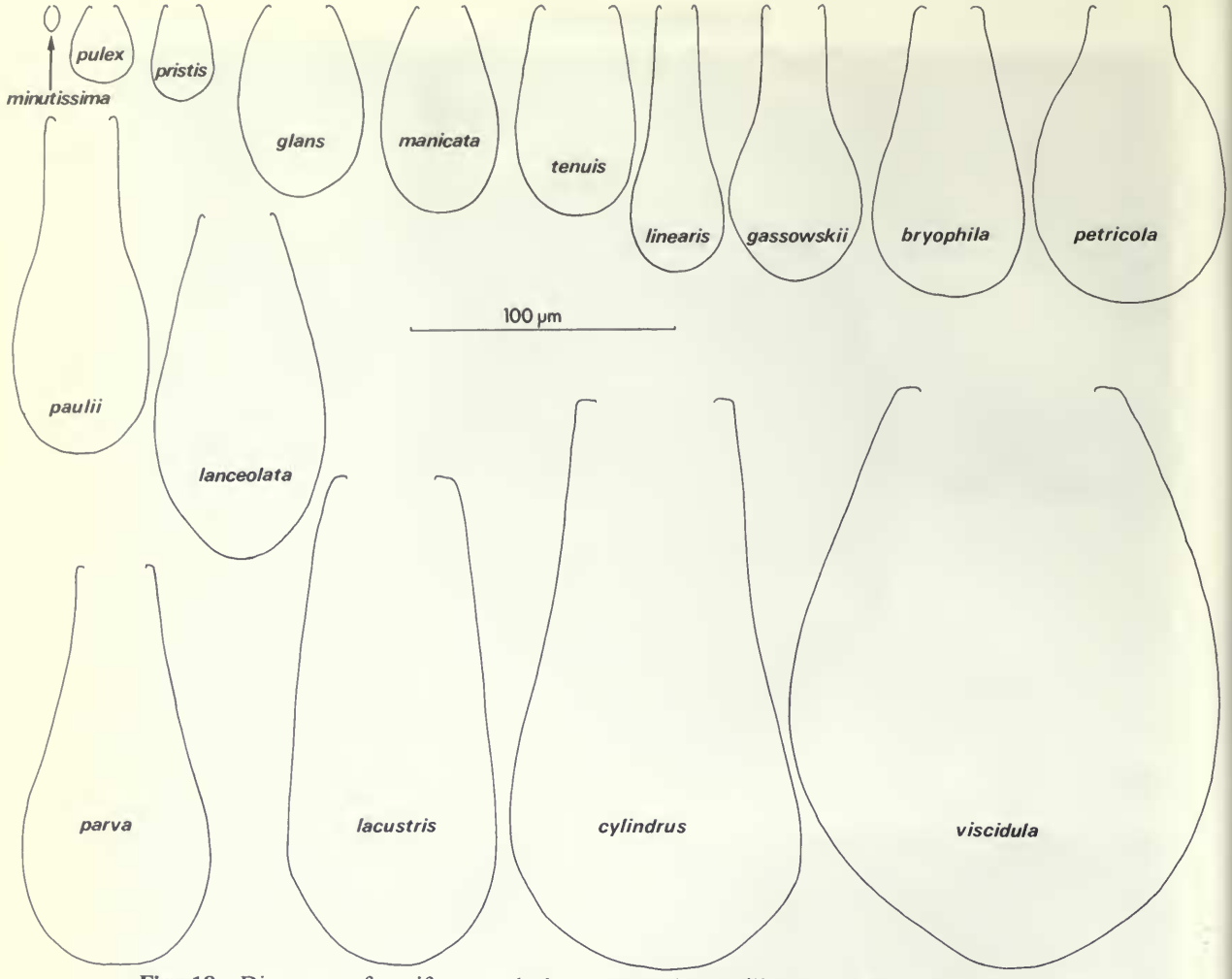

Fig. 18 Diagrams of pyriform and elongate species to illustrate the basic, outline based on measurements given in Table 2.

Table 2 Average dimensions of pyriform specimens listed in Table 1 and illustrated in Fig. 18.

Species	Length	Breadth	Diameter of aperture
D. minutissima	9	7	3
D. pulex	32	25	8
D. pristis	37	25	11
D. glans	71	46	20
D. manicata	77	47	16
D. tenuis	77	44	23
D. linearis	100	35	12
D. gassowskii	102	50	18
D. bryophila	108	58	19
D. petricola	111	72	25
D. paulii	126	50	21
D. lanceolata	128	64	25
D. parva	149	75	24
D. lacustris	183	78	34
D. cylindrus	211	112	45
D. viscidula	217	161	66

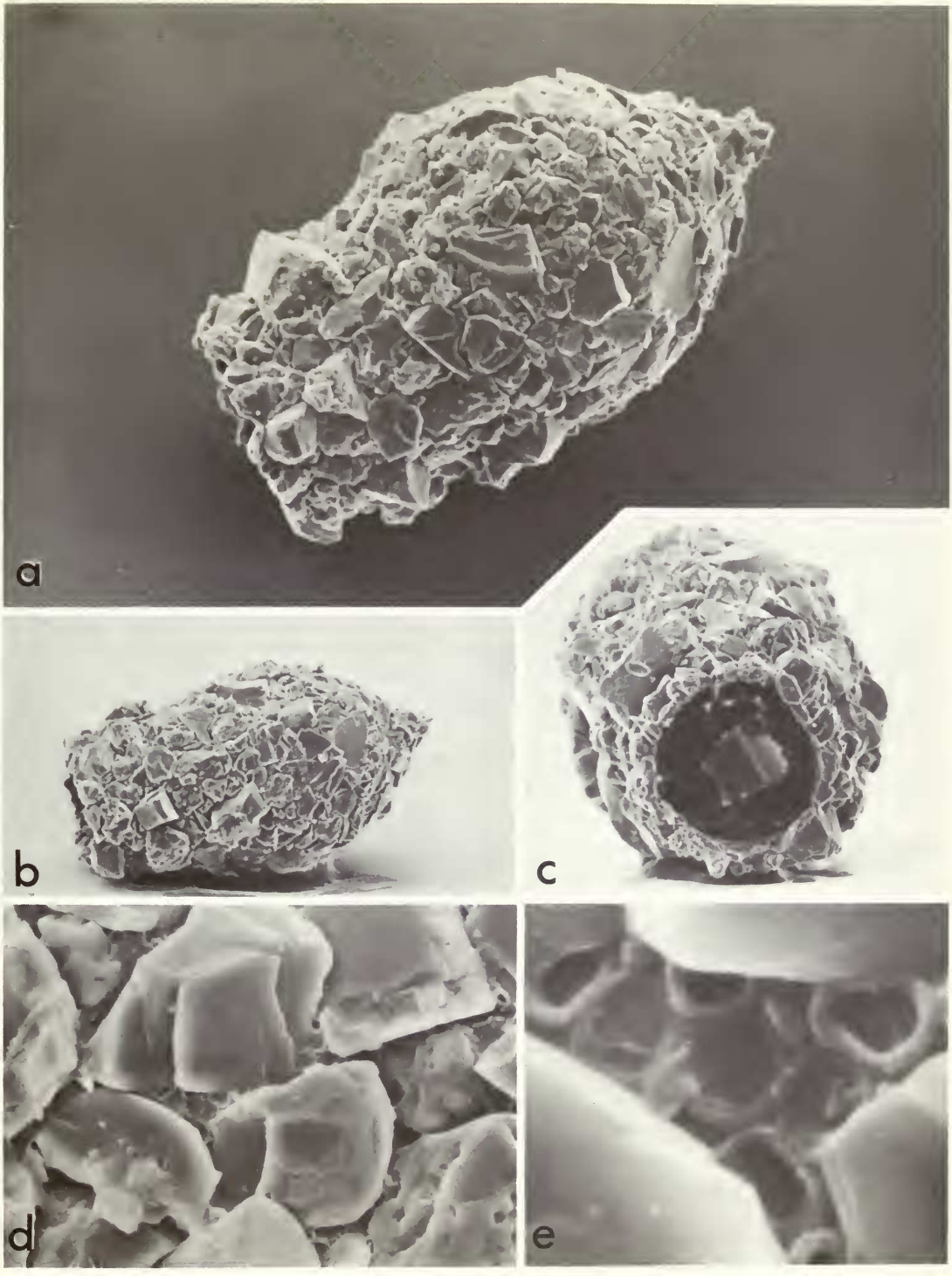

Fig. 19 *Difflugia amphoralis:* a, lateral view ×850; b, lateral view to show even aboral tapering ×500; c, apertural view ×760; d, shell surface showing areas of organic cement ×4500; e, detail of organic cement network ×24 000.

form a network, each mesh of which is about 380–450 nm internal diameter and the raised walls are 130 nm thick, a smooth membrane covers each enclosure (Fig. 19c). The circular aperture is surrounded by a small rim of mainly small particles to give a poorly defined border (Figs. 19a, b & c).

MEASUREMENTS (in μm). A single specimen: body length 109, breadth 62, diameter of aperture 28.

MATERIAL EXAMINED. The specimen was found in *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. British Isles (Cash & Hopkinson, 1909), Tashkent (Pashintowa, 1929).

REMARKS. The structure of the shell in the present specimen differs from the original (Cash & Hopkinson, 1909) by being composed mainly of quartz particles, rather than 'amorphous (?siliceous) scales'. However, it should be noted that the specimens described by Leidy (1879) and quoted as synonyms of this species by Cash & Hopkinson (1909) are also composed mainly of 'quartz sand'.

Difflugia bicruris Gauthier-Lièvre & Thomas, 1958

DESCRIPTION. The shell is elongate ovoid, the sides being almost parallel with a slight tapering towards the aperture and the aboral extremity, the latter is rounded and has two small, equally spaced, protruberances or horns (Figs. 20a & c). It is composed of medium to large pieces of angular quartz, with some small particles being used in shaping the horns (Fig. 20d). The surface is rough but patches of organic cement are seen to form part of the shell matrix (Fig. 20e). Organic cement is arranged in the form of a regular network whose mesh has a diameter of about 300–350 nm and the distance between each enclosure is about 300 nm (Fig. 20f). The aperture is circular and surrounded by an even arrangement of small particles (Fig. 20b).

MEASUREMENTS (in μm). Two specimens: body length 202–207, breadth 95–115, diameter of aperture 41–58.

MATERIAL EXAMINED. Specimens were collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk, in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970).

REMARKS. Slight differences exist between the present specimens and those described by Gauthier-Lièvre & Thomas (1958). They have slightly larger general body measurements, although the proportions are directly comparable, and the horns are reduced in length, 20 μm here compared with 30–33 μm in the African specimens. Nevertheless, the descriptions are in good agreement showing that *D. bicruris* is distinctly ovoid with two aboral spines or horns.

Difflugia distenda nom. nov.

Difflugia acuminata var. *inflata* Penard, 1899

DESCRIPTION. The shell is transparent, pyriform with the aboral extremity acutely curved towards a small central tubular horn (Fig. 21a), although the extent of the angle may be less acute in a few specimens. It has an intermediate smooth surface and thickness, being composed mainly of small to medium pieces of quartz, with occasional diatom frustules added. Areas of organic cement are sometimes seen in the shell matrix as a network (Fig. 21c), with a mesh 350–400 nm in diameter and walls 150–200 nm thick (Fig. 21d). The

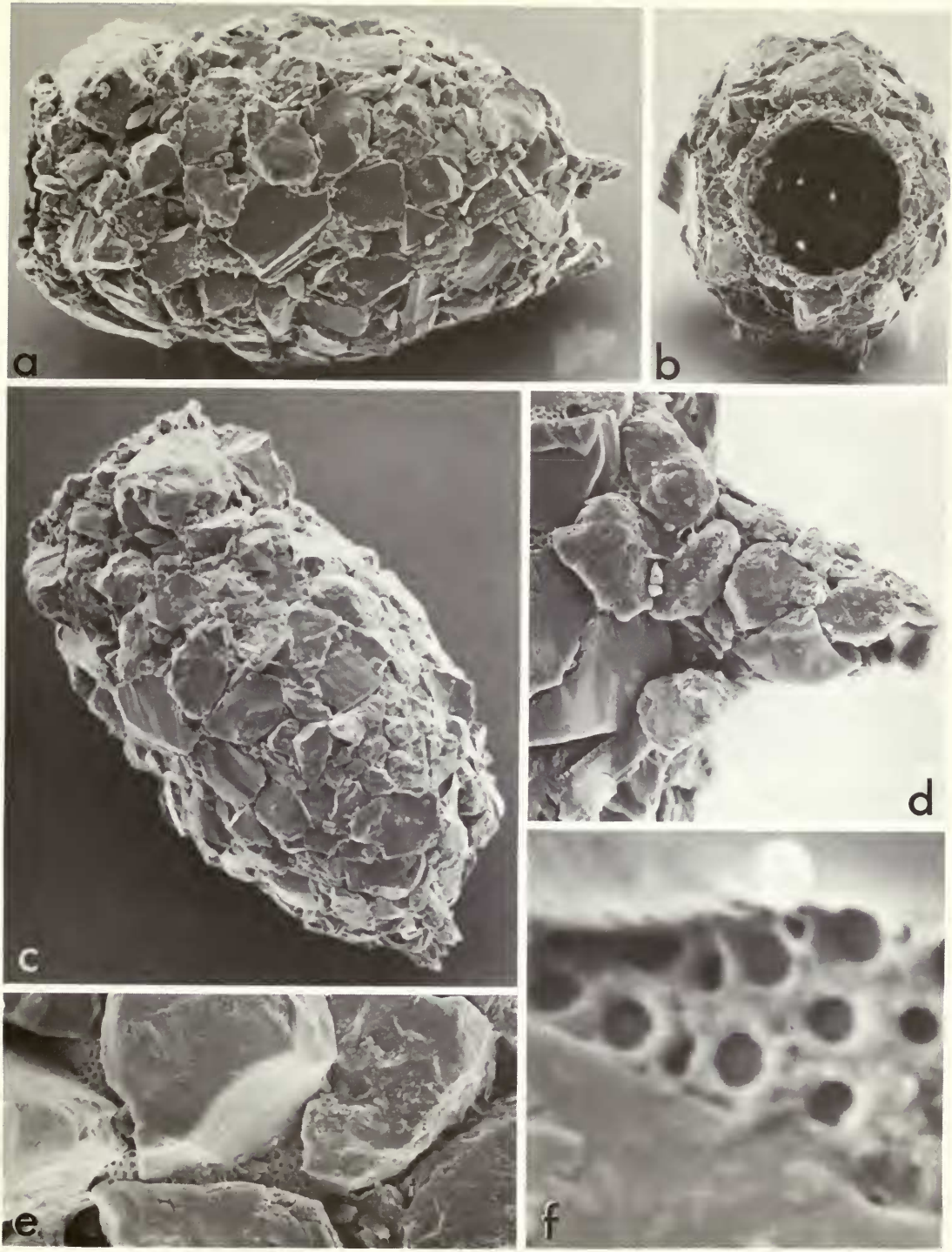

Fig. 20 *Difflugia bicruris:* a, lateral view illustrating the two aboral horns ×420; b, apertural view ×400; c, alternative lateral view with aboral horns not easily seen ×430; d, detail of aboral horn ×2500; e, portion of shell surface showing distribution of organic cement ×2700; f, detail of organic cement network ×25 000.

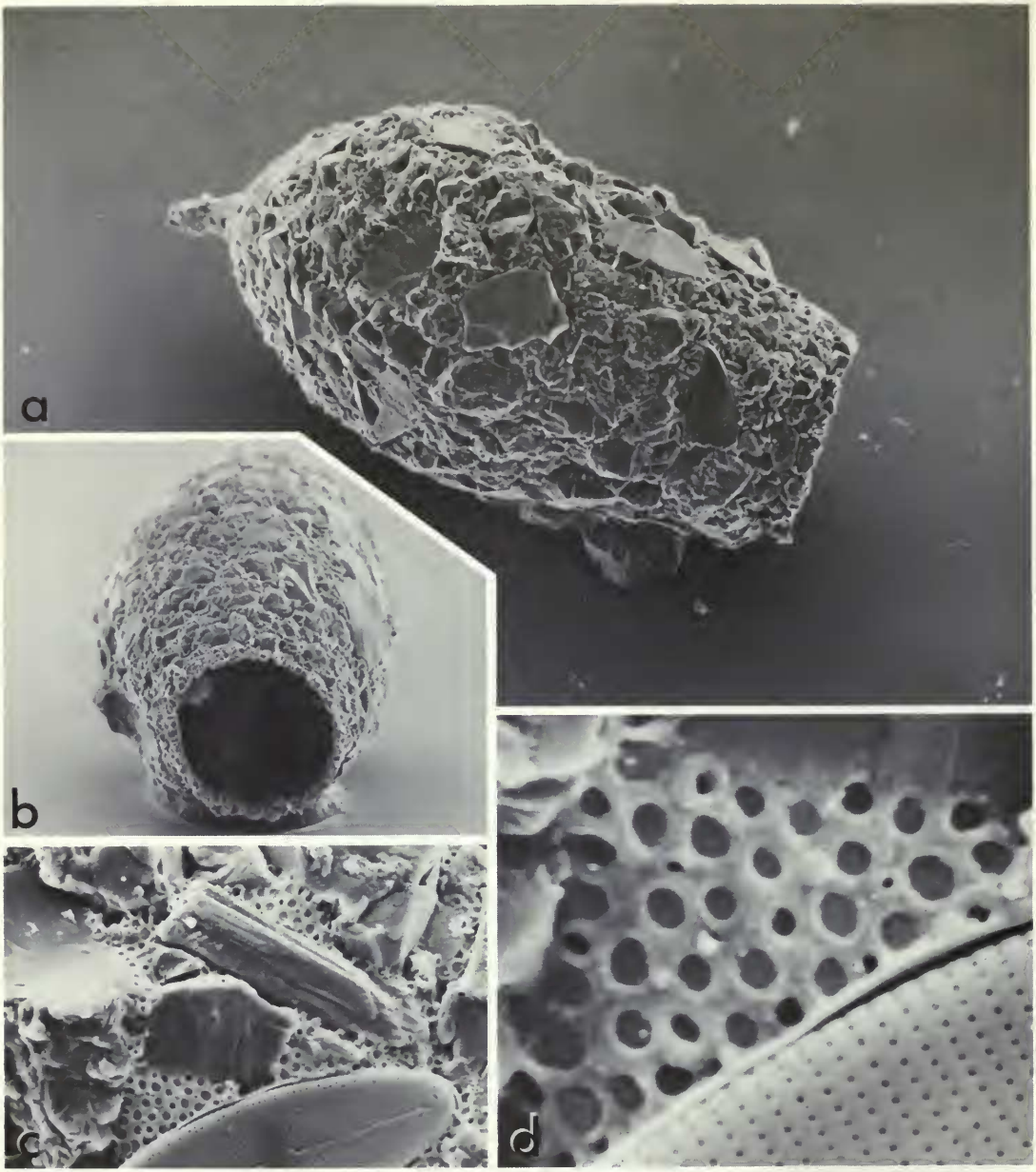

Fig. 21 *Difflugia distenda:* a, lateral view to show small aboral horn ×430; b, apertural view ×350; c, shell surface showing large areas of organic cement ×2400; d, detail of organic cement network ×11 000.

aperture is circular and usually surrounded by an even arrangement of small particles (Fig. 21b).

MEASUREMENTS (in μm). Based on ten specimens: body length 217–270, breadth 109–135, diameter of aperture, 58–64; B/L 0·53 ± 0·04, d/L 0·26 ± 0·02.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Austria (Laminger, 1971, 1973*b*), Belgium (Chardez, 1961*a*), British Isles (Cash & Hopkinson, 1909), Congo (Chardez, 1964; Gauthier-Lièvre & Thomas, 1958), France (Deflandre, 1962*b*; Thomas & Mabille, 1956), Gabon (Gauthier-Lièvre & Thomas, 1958), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Mexico (Laminger, 1973*b*), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970; Moraczewski, 1965), Switzerland (Penard, 1902), Tashkent (Pashintowa, 1967).

REMARKS. The variations of *D. acuminata*, and its twelve varieties has recently been illustrated by Chardez (1961). More recently it has been shown (Ogden, 1979) that *D. acuminata* Ehrenberg, 1838 has a distinctive elongate shape and an apparently unique organic cement pattern. Specimens described as var. *inflata* differ from this species in shape, size and organic cement pattern, the former is clearly demonstrated when the measurements are expressed as ratios, the comparable ratios for *D. acuminata* are B/L 0·36 ± 0·03 and d/L 0·15 ± 0·03 (Ogden, 1979).

The specimens described here agree well with Penard's (1899, 1902) original descriptions, and the differences from *D. acuminata* are considered sufficient to warrant specific designation. Our normal practise is to raise the variety name to specific rank, but on this occasion it is impracticable as the terminology *inflata* has been used several times in connection with specimens of *Difflugia,* for example *D. curvicaulis* var. *inflata* Decloitre, 1951.

ETYMOLOGY· The specific name has been selected to reflect the inflated condition of the shell (L. *distenda* = swell out).

Difflugia labiosa Wailes, 1919

Difflugia amphora Leidy 1879 of Penard, 1901; 1902 & 1905

DESCRIPTION. The shell is opaque or dark brown, ovid or elongate ovoid, tapering from the mid-body region sharply to the rounded or pointed aboral extremity and more gradually towards the aperture (Fig. 22a). It is relatively thick and composed of quartz pieces so arranged that small particles fill the interstices between the larger pieces which form a mainly smooth surface (Fig. 22d). Organic cement is seen infrequently but is in the form of a network, each mesh being about 250–350 nm in diameter and is usually covered by a smooth membrane (Fig. 22e). The aperture is roughly circular but is sinuous with as many as six or seven undulations or lobes (Fig. 22b). It is slightly recessed into the main body, as though it was surrounded by a groove, the margin or lips, are thin and bordered by tiny particles of quartz. (Fig. 22b & c).

MEASUREMENTS (in μm). Based on five specimens: body length 150–211, breadth 112–158, diameter of aperture 50–63.

MATERIAL EXAMINED. Specimens were collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Austria (Laminger, 1971, 1975), Belgium (Chardez, 1980), British Isles (Cash *et al.,* 1919; Ogden & Hedley, 1980), Czechoslovakia (Ertl, 1965; Štěpánek, 1952, 1967), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Grospietsch, 1958; Schönborn, 1962*a, & b*), Netherlands (Hoogenraad & Groot, 1940), Poland (Moraczewski, 1961, 1965), Russia (Kourov, 1925), South Africa (Oye, 1931), Switzerland (Penard, 1902), Venezuela (Deflandre 1926*a*; Grospietsch, 1975).

REMARKS. There has been some confusion over the correct name for this species, most recent authors using *D. amphora* Leidy, 1879, basing their identifications on the description given by Penard (1902). However, this name is preoccupied as it was used by Ehrenberg (1854, 1872) to describe a specimen which is no longer considered to be a species of *Difflugia*. It

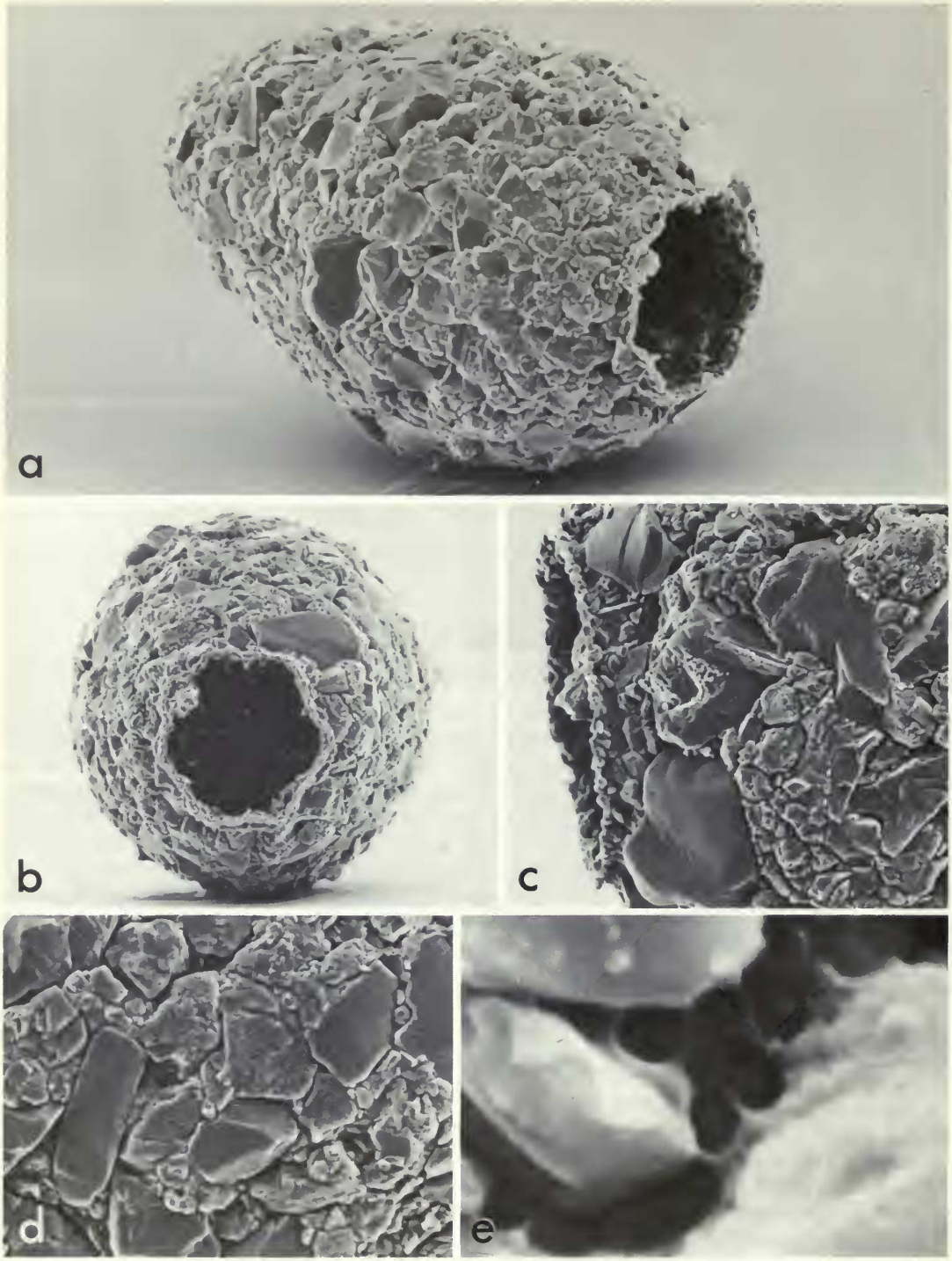

Fig. 22 *Difflugia labiosa:* a, latero-apertural view to show arrangement of particles ×580; b, apertural view illustrating the undulations or lobes ×470; c, lateral view of aperture to show slight groove and small particles on margin ×990; d, portion of shell surface showing the close packing of particles ×1300; e, detail of organic cement ×24 000.

follows that the later reports by Leidy (1874, 1879) default for the same reason. The latter report being more confusing by quoting *D. amphora* as a synonym of *D. urceolata*, whilst giving a figure of *D. ureceolata* var. *amphora*. Wailes (in Cash *et al.*, 1919) noted these earlier reports and proposed the new name *D. labiosa*, giving Penard's (1901, 1902, 1905) reports as synonyms. Earlier, Cash & Hopkinson (1909) had suggested that part of Leidy's (1879) description of *D. urceolata* var. *amphora* was a synonym of their new species *D. amphoralis*. The specimens described here are in good agreement with Penard (1902) who gave a range of body lengths 150–270 μm, but usually about 200–210 μm, and Wailes who suggested that it was a rare species from his single 265 μm long specimen.

This species is distinct in its ovoid-conical shape plus the lobed aperture with distinct margin and recessed base.

Difflugia mamillaris Penard, 1893

DESCRIPTION. The shell is colourless or hyaline, ovoid elongate, swollen or arched in the mid-region but tapering at both extremities, to give a rounded protruberance aborally and gradually near the aperture to give a slightly pronounced neck (Fig. 23a). Irregularities in general shape are not uncommon, for example one specimen although tapered did not have an aboral protruberance, whilst another (Fig. 23c) tapered markedly from the mid-body region. It is composed mainly of small to medium pieces of quartz so arranged that the larger particles tend to be in the mid-body region whilst the extremities have the smaller particles, overall it usually produces an intermediate thickness of a single layer and a relatively smooth outline. Organic cement occurs in small patches as a network, which has walls about 80–130 μm thick between each mesh but sometimes 230 μm thick at junctions. Each mesh is about 250nm in diameter and is covered by a smooth membrane which is distinct in having three or four small white spots on the surface of each enclosure (Figs. 23d & e). The aperture is circular, composed of small particles, and roughly finished so that the margin appears uneven or serrated (Fig. 23b).

MEASUREMENTS (in μm). Based on twenty-three specimens: body length 93–111, breadth 54–72, diameter of aperture 23–31.

MATERIAL EXAMINED. Specimens were collected from a sample of aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Austria (Laminger, 1975), Congo (Chardez, 1964), Czechoslovakia (Štěpánek, 1967), Germany (Grospietsch, 1957), Switzerland, (Penard, 1901), Venezuela (Grospietsch, 1975).

REMARKS. This species was initially described by Penard (1893) and redescribed in more detail by the same author (Penard, 1902). The present specimens are in good agreement with the latter description, including measurements which gave the body length as being generally between 90–110 μm with a few large specimens up to 130 μm long. More recently, Grospietch (1957) has shown a similar regularity in size of specimens from Lake Maggiore, giving length 90–113 μm and breadth 48–63 μm. Penard (1902) suggested that this species was rare in Swiss Lakes, and this appears to be the case in other localities judging by its reported incidence. Nevertheless, if the two recent reports (Grospietch, 1957 and the present) are used as indicators, it would appear that when present this species is usually abundant.

D. mamillaris is distinct in outline, even though the thin structure may be subject to distortion, and the unusual organic cement pattern.

Difflugia microclaviformis (Kourov, 1925) comb. nov.

Difflugia oblonga var. *microclaviformis* Kourov, 1925

DESCRIPTION. The shell is brown, pyriform with a distinct aboral protruberance (Fig. 24a). It

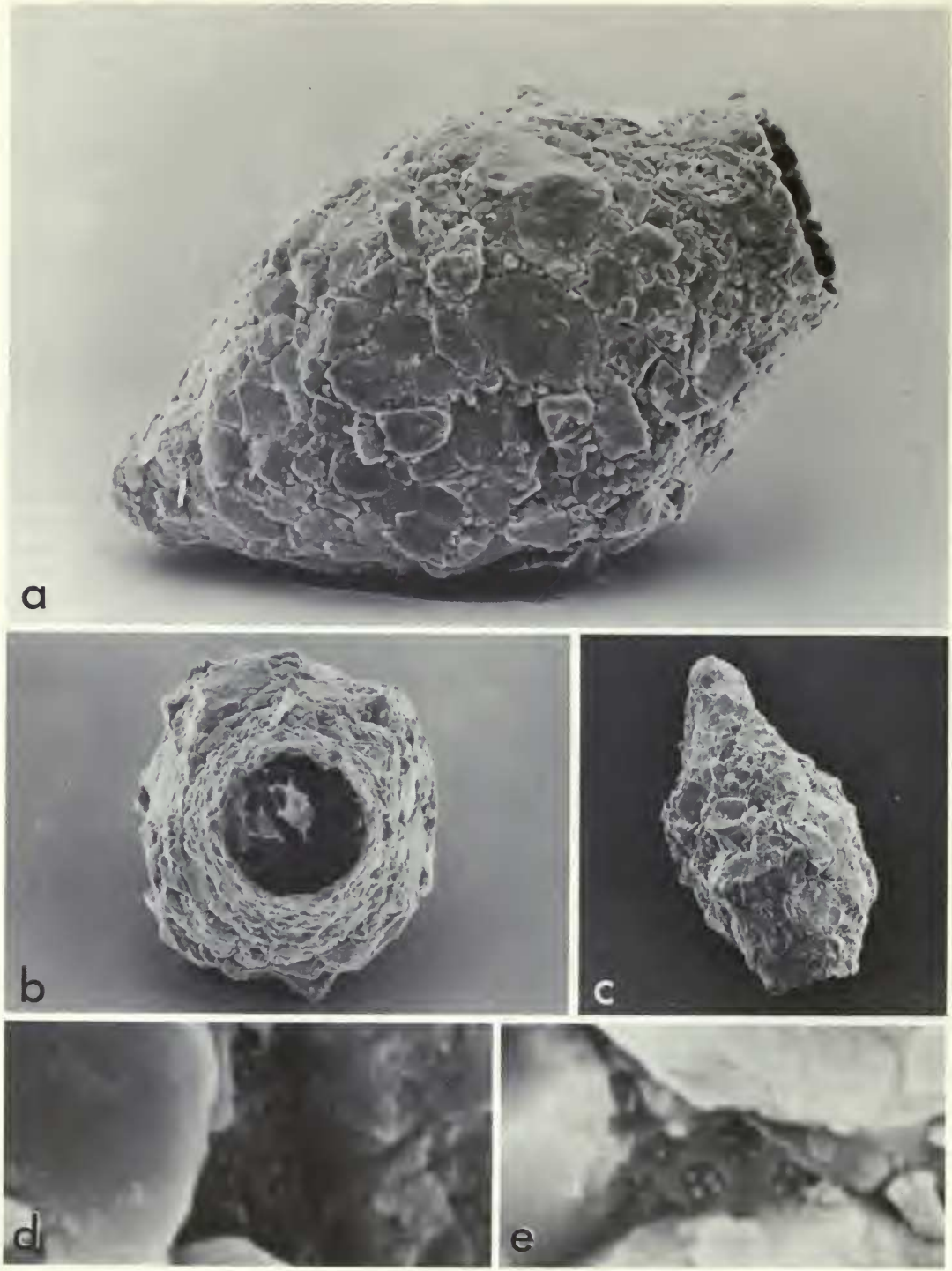

Fig. 23 *Difflugia mamillaris:* a, lateral view ×1100; b, apertural view ×790; c, lateral view of irregular shaped shell ×440; d and e, detail of organic cement network, note the small white spots in each enclosure which is a regular feature ×24 000.

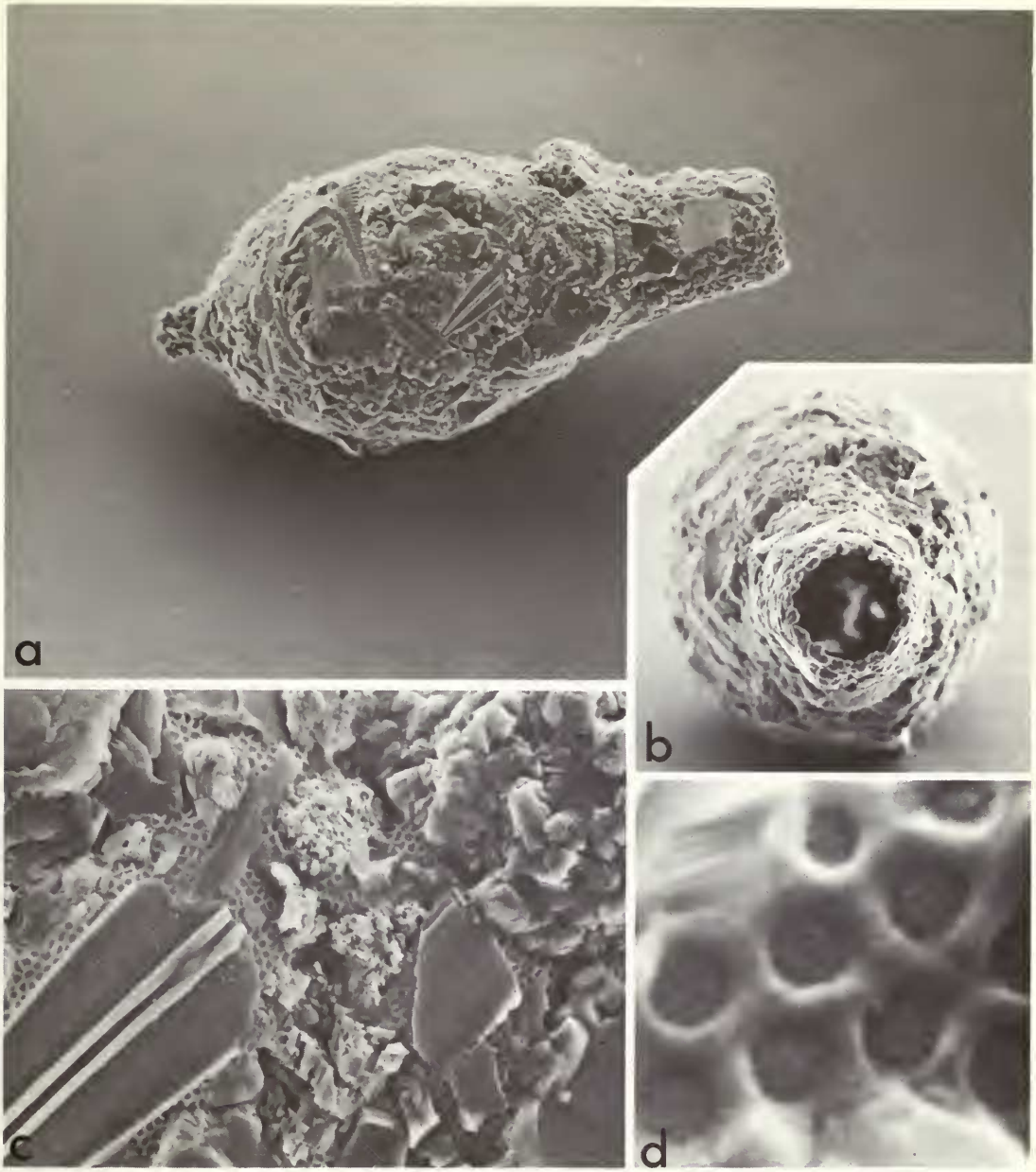

Fig. 24 *Difflugia microclaviformis:* a, lateral view ×230, b, apertural view ×530; c, shell surface illustrating the arrangement of particles and organic cement ×2600; d, detail of organic cement network, note the regular distribution of small pores in each enclosure ×33 000.

is composed of small to medium pieces of quartz, some flattish diatom frustules, and a network of organic cement is often seen as part of the shell matrix (Fig. 24c). The result is a smooth surface and a well defined outline. The mesh of the organic cement has a diameter of 300 nm with walls 150 nm thick, and a smaller network, with pores about 30 nm in diameter, covers each mesh enclosure (Fig. 24d). The aperture is circular and surrounded by small particles (Fig. 24b).

MEASUREMENTS (in μm). Based on two specimens: body length 202–206, breadth 88–89, diameter of aperture 27–28.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire, in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Vucetich, 1978), Austria (Laminger, 1973*b*), Congo (Gauthier-Lièvre & Thomas, 1958), France (Thomas, 1954), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Mexico (Laminger, 1973*a*), Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Spain (Gracia, 1972*a*).

REMARKS. This species when initially described (Kourov, 1925) had a body length not greater than 185 μm, whereas Gauthier-Lièvre & Thomas, 1958 gave dimensions similar to those given here. It is redescribed to show its marked similarity to *D. claviformis*, lack of material prevents a complete comparison and the identification must be treated as tentative. *D. microclaviformis* appears to differ from *D. claviformis* (see Ogden, 1979) in size and possibly the organic cement pattern.

Difflugia molesta Penard, 1902

DESCRIPTION. The shell is brown, ovoid or ovoid-elongate, sometimes with a small apertural collar and arched aborally (Fig. 25a). It is composed of a mixture of quartz particles and diatom frustules, the former usually being predominant. Organic cement is seen as a network between particles, either as part of the shell matrix or occasionally at junctions. The rings that form the network are about 650–750 nm internal diameter with the dividing wall being 100–150 nm thick, a second thin, inner wall lies close to the main wall and in the illustrated specimen the covering membrane is either holed or figured (Fig. 25c). The aperture is roughly circular, irregular in outline, and mainly surrounded by small particles (Fig. 25b).

MEASUREMENTS (in μm). Based on four specimens: body length 106–114, breadth 61–87, diameter of aperture 28–43.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Switzerland (Penard, 1902).

REMARKS. These specimens are tentatively identified here as *D. molesta*, the query arising due to their similarity with *D. amphoralis*. Of the four specimens examined, the smallest (Fig. 25a) bears the closest resemblance being slim, with a small aperture and differing in the absence of a pointed aboral protruberance. The three broader specimens have a wider aperture, a narrow neck and are arched aborally. In addition, there are differences in the organic cement patterns between the two species, but altogether there is insufficient information to satisfactorily resolve the problem.

Difflugia tricornis (Jung, 1936) comb. nov.

Difflugia elegans forma *tricornis* Jung, 1936

DESCRIPTION. The shell is pyriform, with a slight broadening near the aperture, and is characterised by three, evenly spaced, aboral spines (Fig. 26a). The surface is rough and mainly composed of a mixture of medium and large pieces of angular quartz, the spines have medium particles at their wide bases but small particles are used progressively as they taper to a point. Small areas of organic cement are seen between the particles (Fig. 26c), usually in the form of a regular network (Fig. 26d), having a mesh between 350–400 nm internal

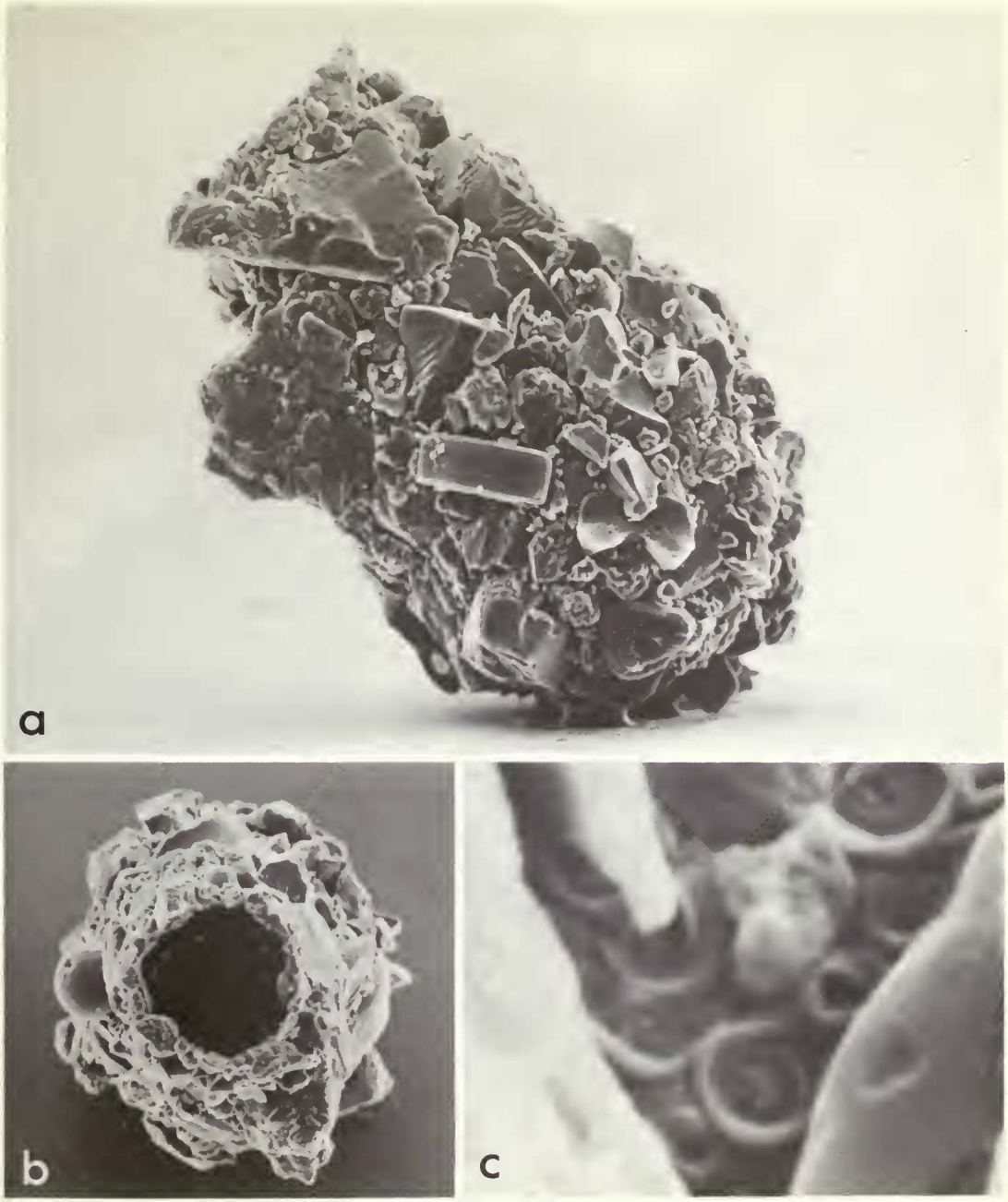

Fig. 25 *Difflugia molesta:* a, lateral view ×910; b, apertural view ×740; c, detail of organic cement to show arrangement of rings and figured centre ×24 000.

diameter and dividing walls about 150 nm thick although at some junctions there are larger areas. The aperture is circular and surrounded by an irregular assortment of particles (Fig. 26b).

MEASUREMENTS (in μm). One specimen: body length 116, breadth 82, diameter of aperture 40.

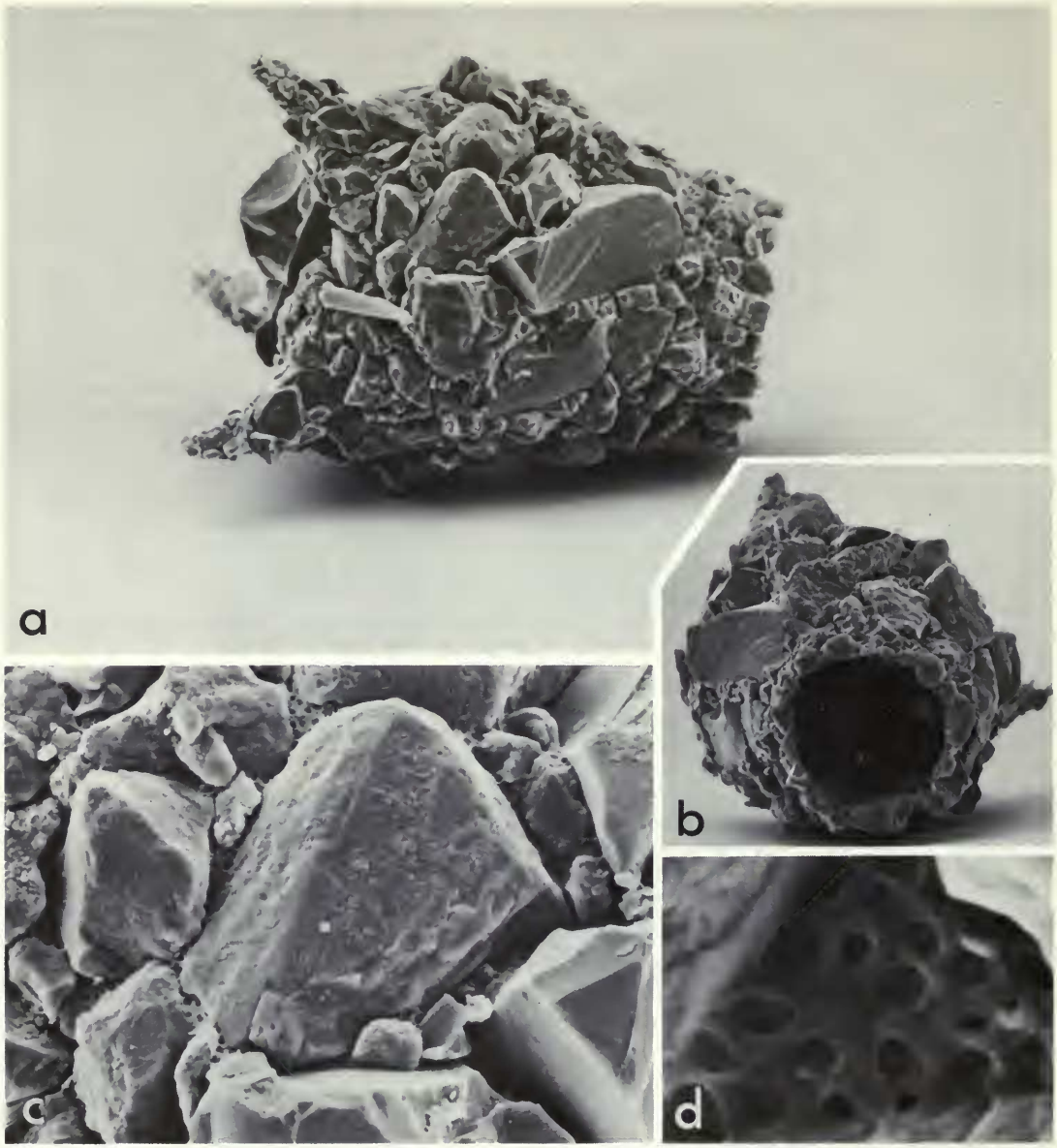

Fig. 26 *Difflugia tricornis:* a, lateral view to show the three equally spaced aboral spines ×690; b, apertural view ×530; c, portion of shell surface showing small areas of organic cement ×2300; d, detail of organic cement network ×14 000.

MATERIAL EXAMINED. The specimen was collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Germany (Jung, 1936), Sudan (Gauthier-Lièvre & Thomas, 1958).

REMARKS. In the earlier descriptions (Jung, 1936; Gauthier-Lièvre & Thomas, 1958) the specimens resembled *D. elegans* except for the three aboral spines which were stated to be randomly placed, although Jung (1936) cited Penard's figures referring to much smaller animals. Differences in the shape and structure of *D. elegans* examined recently by the

author (Ogden, 1979; Ogden & Hedley, 1980) have been confined to the size and structure of the single aboral spine or horn, whilst the body length was usually of a standard size 110–160 μm.

The present specimen has three, equally spaced, aboral spines and the body breadth is markedly wider, features that are considered sufficiently different from *D. elegans* to warrant a specific designation. The earlier reports are placed, with reservations, in synonymy.

Difflugia ventricosa Deflandre, 1926

DESCRIPTION. The shell is colourless, elongate, with a slight swelling in the aboral half of the body which then tapers to a sharp point (Fig. 27a). It is composed of a mixture of quartz, diatom frustules and flagellate cysts to give a thin, irregular surface. Organic cement is frequently seen between particles in the form of a network (Fig. 27c), made of rings about 600–680 nm in diameter with walls 180–250 nm thick (Fig. 27d). In some instances the rings are fused and appear to have lost or merged their walls (Fig. 27e). The aperture is circular and usually surrounded by small particles (Fig. 27b).

MEASUREMENTS (in μm). Two specimens: body length 177–199, breadth 64–66, diameter of aperture 30–31.

MATERIAL EXAMINED. The specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Belgium (Chardez, 1973), Congo (Gauthier-Lièvre & Thomas, 1958), France (Thomas & Mabille, 1956), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Venezuela (Deflandre, 1926*a*).

REMARKS. A redescription of *D. ventricosa* has recently been given by Chardez (1973) who compared it with other species having a pointed aboral extremity. It is interesting to note that he made no comparison with *D. venusta*, although from the description given here (below) there would seem to be some similarities. The tabulated measurements given by Chardez (1973) from earlier descriptions, are in good agreement with the exception of those given by Thomas & Mabille (1956).

This species is distinct in having a thin, elongate outline which is sharply pointed aborally.

Difflugia venusta (Penard, 1902) comb. nov.

Difflugia pyriformis var. *venusta* Penard, 1902
Difflugia oblonga var. *venusta* (Penard, 1902) Cash & Hopkinson, 1909

DESCRIPTION. The shell is pale yellow or hyaline, cylindrical, gradually swelling from the aperture for about two-thirds of the body length to the broadest diameter and then tapering sharply in the last third to the bluntly pointed apex (Fig. 28a & b). It is composed mainly of small to medium pieces of quartz and diatom frustules arranged to give a relatively regular, intermediate smooth, outline apart from the occasional addition of a larger angular piece of quartz or diatom frustule. Small areas of organic cement are sometimes visible as a thick walled network with a covered mesh (Fig. 28d), but more often as thick walled rings about 450–600 nm in diameter and walls 150–220 nm (Fig. 28c). The aperture is usually circular and surrounded by small particles that give it an irregular margin (Fig. 28c).

MEASUREMENTS (in μm). Based on three specimens: body length 174–188, breadth 68–76, diameter of aperture 30–32.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Argentina (Dioni, 1970), Belgium (Chardez & Gaspar, 1976),

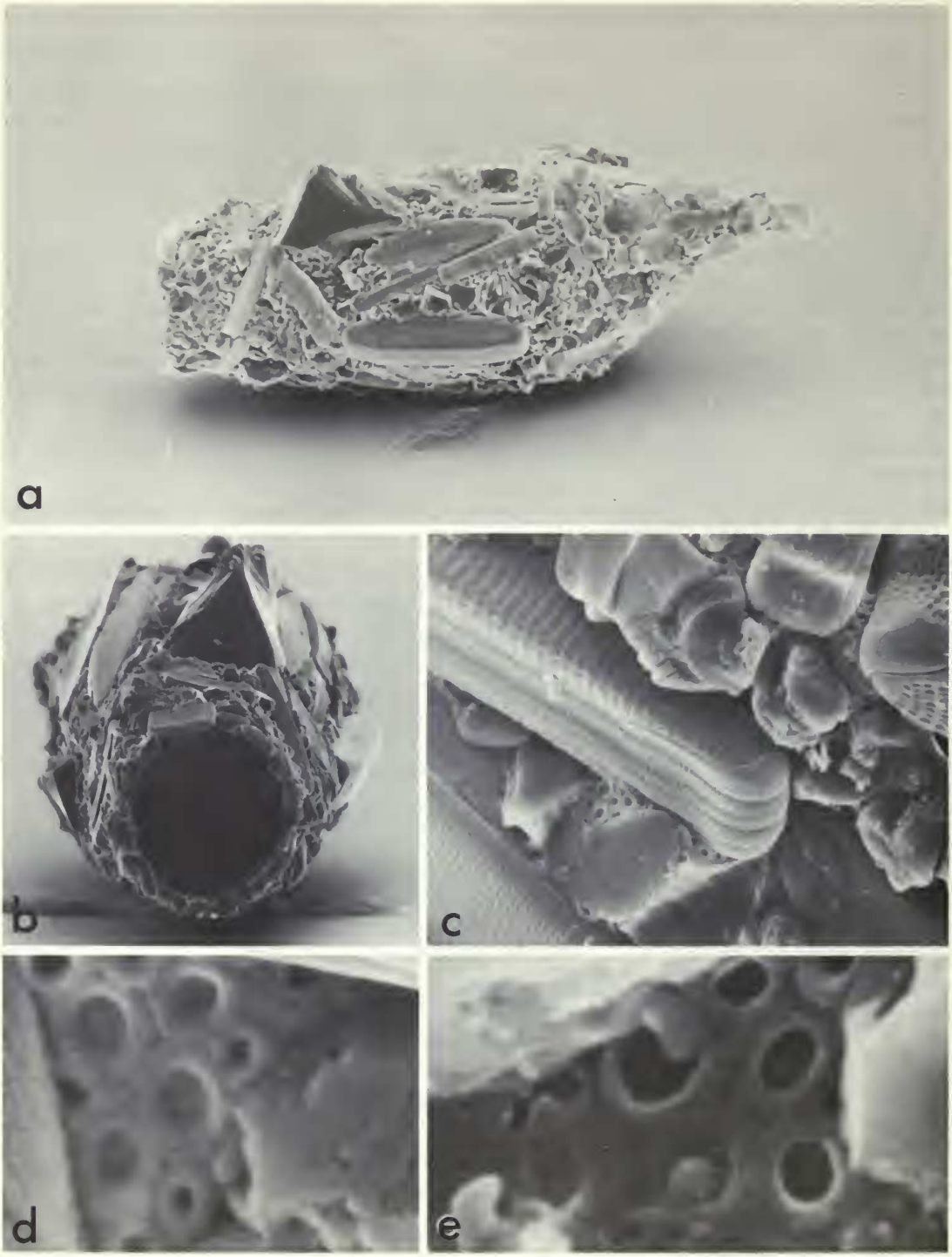

Fig. 27 *Difflugia ventricosa:* a, lateral view to illustrate tapering of aboral spine ×520; b, apertural view ×760; c, shell surface showing small areas of organic cement ×4700; d, detail of organic cement network of rings ×24 000; e, organic cement network with fused rings ×28 000.

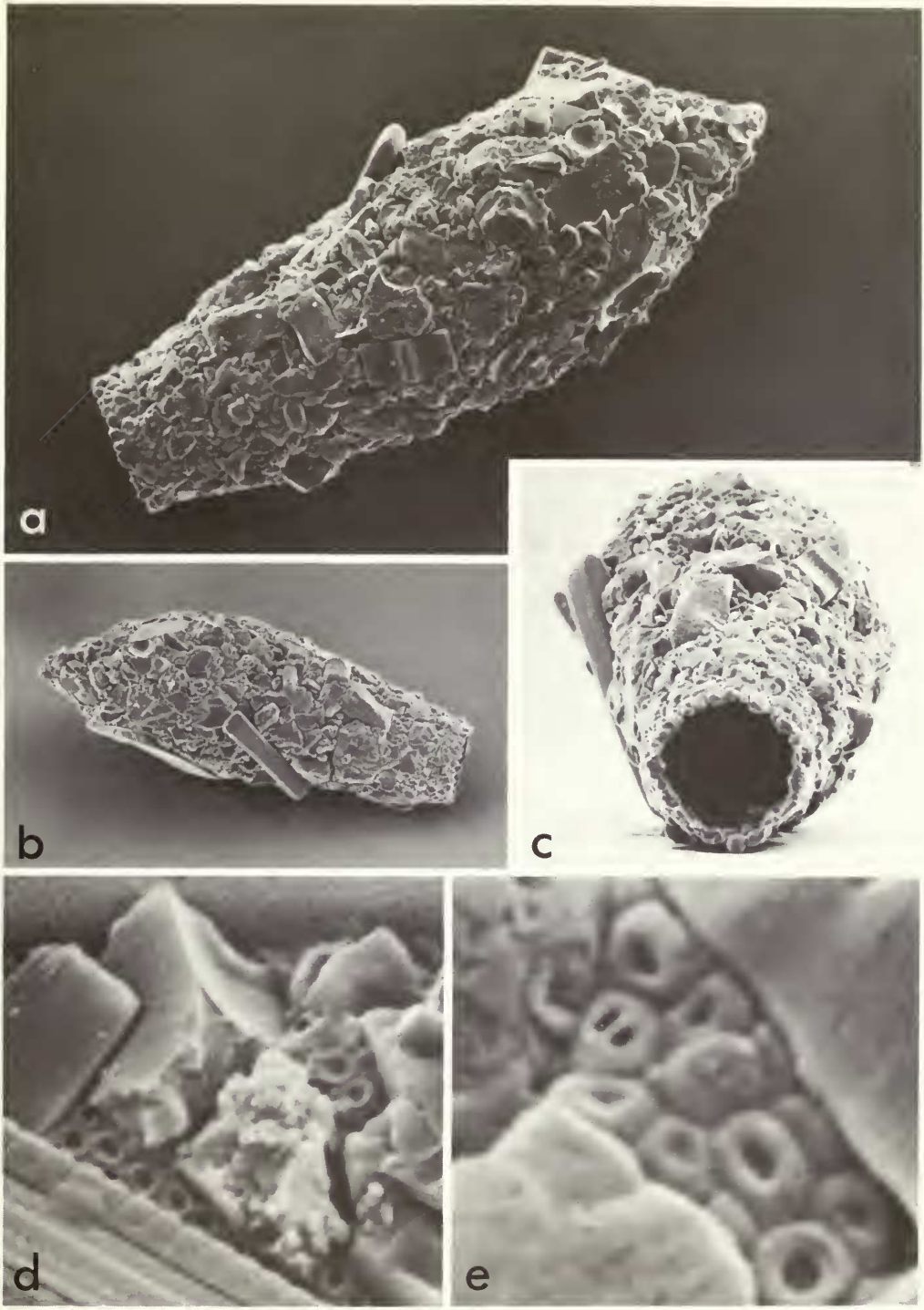

Fig. 28 *Difflugia venusta:* a and b, lateral views to show sharp tapering of aboral region ×570 and ×340; c, apertural view ×590; d, shell surface showing distribution of organic cement ×9200; e, detail of organic cement network ×24 000.

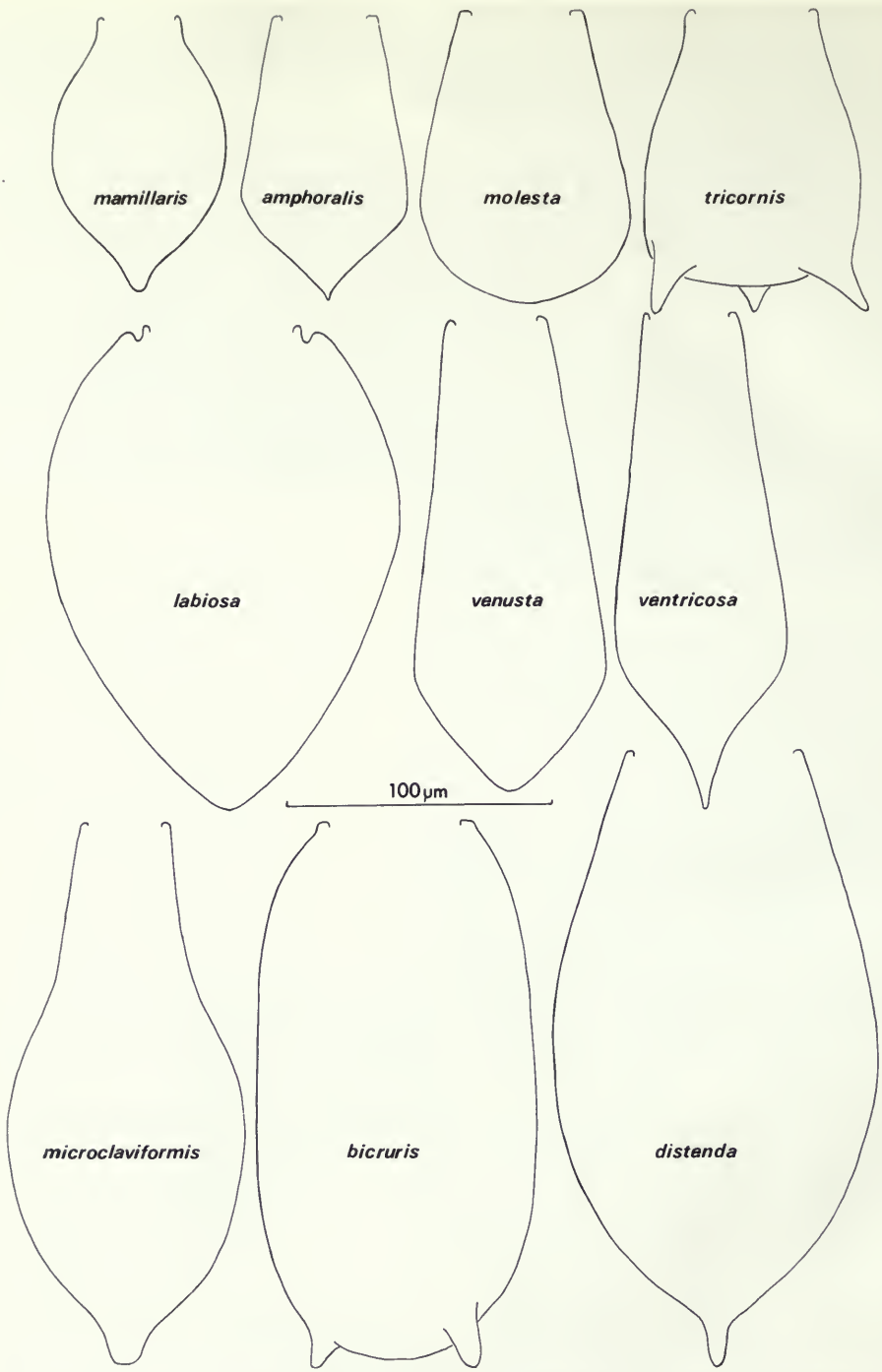

Fig. 29 Diagrams of pointed species or those with protruberances to illustrate the basic outline, based on measurements given in Table 3.

Table 3 Average dimensions of pointed species or those with protruberances used to give basic outlines illustrated in Fig. 29

Species	Length	Breadth	Diameter of aperture
D. mamillaris	103	65	27
D. amphoralis	109	62	32
D. molesta	110	73	37
D. tricornis	116	82	40
D. labiosa	183	132	55
D. venusta	179	71	31
D. ventricosa	188	65	30
D. microclaviformis	204	88	27
D. bicruris	205	106	50
D. distenda	230	122	60

France (Thomas, 1954), Haute Volta, W. Africa (Gauthier-Lièvre & Thomas, 1958), Switzerland (Penard, 1902).

Remarks. The present specimens agree well with the descriptions given by Penard (1902), Cash & Hopkinson (1909) and Gauthier-Lièvre & Thomas (1958) who considered it a variety of *D. pyriformis/oblonga,* although the shells described by Cash & Hopkinson (1909) were slimmer than those reported here and by Gauthier-Lièvre & Thomas (1958).

This species is distinct in the graceful outline with bluntly pointed aboral extremity and shell structure.

Ovoid or spherical species

Difflugia ampullula Playfair, 1918

Description. The shell is hyaline, ovoid and circular in cross section (Fig. 30a). It has a medium thickness and is composed mainly of small to medium pieces of quartz, arranged to give a clean outline with a smooth surface. Small areas of organic cement in the form of a network, are often seen as part of the shell structure (Fig. 30d). The mesh of the network is small about 300–350 nm in diameter with thin walls 50–100 nm thick, and an even smaller distinctive network covering each mesh enclosure (Figs. 30e & f). The aperture is circular, surrounded by a slightly raised collar of small particles, and the edge of the collar is often irregular (Figs. 30b & c).

Measurements (in μm). Range of 39 specimens: body length 54–95, breadth 35–72, diameter of aperture 16–29.

Material examined. Specimens were collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

Geographical distribution. Australia (Playfair, 1918).

Remarks. The specimens described here differ slightly from the original description (Playfair, 1918) in the absence of a 'minute, pointed apiculate process' on the aboral extremity. However, this process was reported as being present sometimes, and as there is otherwise good agreement between the two reports, the specimens are designated as *D. ampullula.*

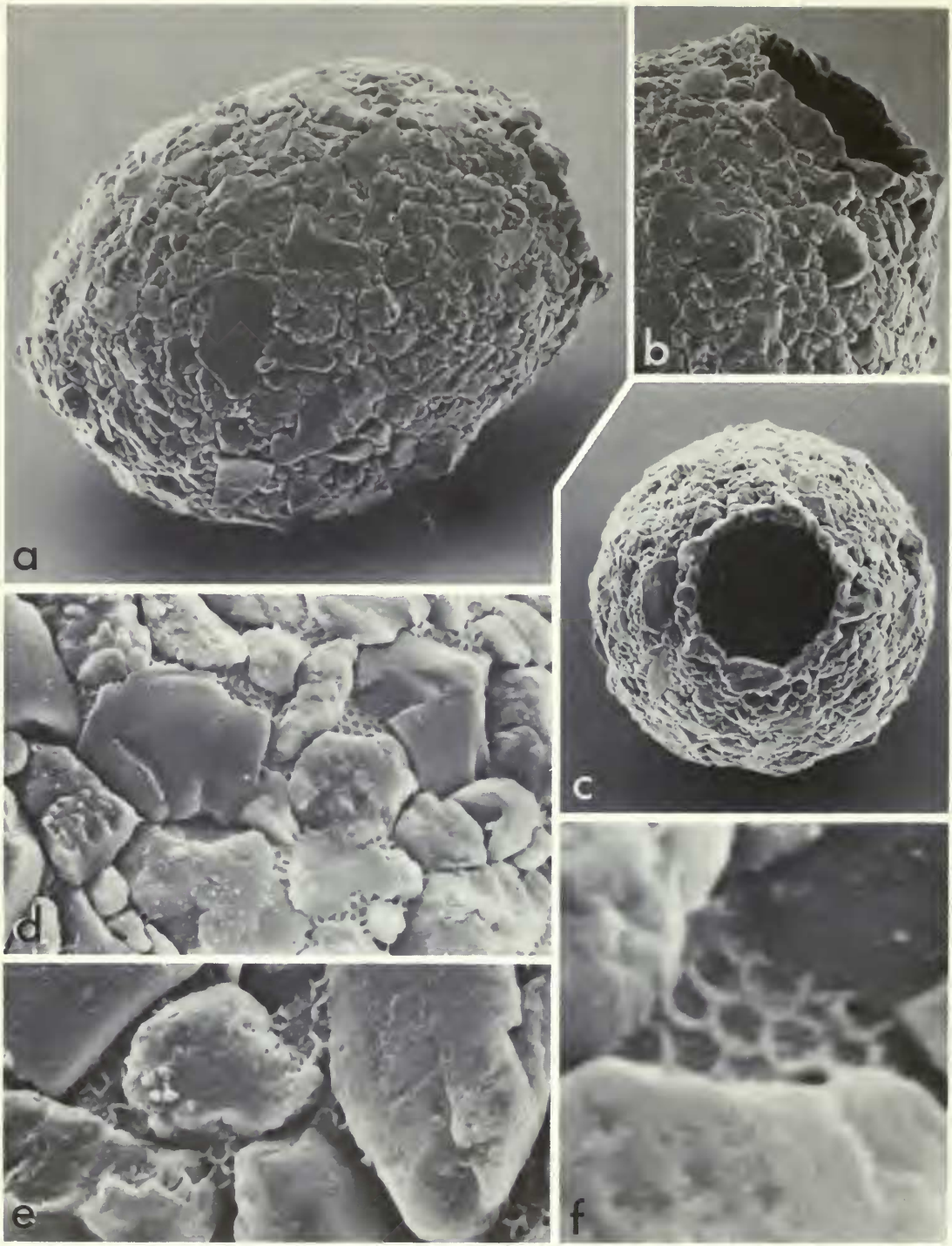

Fig. 30 *Difflugia ampullula:* a, lateral view ×1000; b, latero-apertural view of aperture to illustrate the small collar ×1200; c, apertural view ×770; d, portion of shell surface to show the arrangement of particles and organic cement ×5000; e, detail of shell surface ×7700; f, small area of organic cement network, note that each enclosure has an inner network ×25 000.

Difflugia angulostoma Gauthier-Lièvre & Thomas, 1958

DESCRIPTION. The shell is transparent, spherical and composed mainly of diatom frustules (Fig. 31a & b). The particles are packed close together with many overlapping, to give a rough surface. Organic cement is seen infrequently as small strands between particles (Fig. 31c). The aperture is usually circular (Fig. 31a), but it may have irregularities depending on the arrangement of surrounding diatom frustules.

Two groups of specimens with identical shell features but differing dimensions were examined, the 'a' specimens are from all four listed localities and 'b' specimens are from Three Shires Stone only.

MEASUREMENTS (in μm)

	body length	breadth	diameter of aperture	B/L	d/L
8 specimens 'a'	40–56	40–48	18–23	0·94±0·06	0·42±0·06
8 specimens 'b'	60–82	50–73	28–51	0·87±0·09	0·56±0·05

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at four localities: Cranes Moor in May, 1977, Holmsley in May, 1978 both in the New Forest, Hampshire; Three Shires Stone, Wrynose Pass and Lanthwaite, both in Cumbria, June, 1979.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Vucetich, 1973*a* & *b*), Congo (Gauthier-Lièvre & Thomas, 1958).

REMARKS. This species was described by Gauthier-Lièvre & Thomas (1958), from specimens found in Algeria, who considered that it differed from *D. minuta* by the large size of the aperture, quoted as being about one-third of the breadth in diameter, and the covering diatoms. Both sets of the present specimens, 'a' and 'b', agree well with this description, having a large aperture about half the breadth diameter and are composed of diatoms. The 'b' specimens share almost similar dimensions to *D. angulostoma,* the latter having a body length 60–95 μm and aperture 30–45 μm, whereas the 'a' specimens are generally smaller. The difference in size between specimens 'a' and 'b' is more apparent when the ratios d/L are compared, such differences are usually significant. However, lack of similar data from the original description of *D. angulostoma* does not allow a comparison to be made. In the absence of this information and the otherwise similarity of the two groups of specimens, they are both designated as *D. angulostoma.*

Difflugia decloitrei Godeanu, 1972

Difflugia levanderi Playfair, 1918 (in part)
Difflugia acuminata Levander, 1894 (in part)

DESCRIPTION. The shell is transparent, ovoid, tapering evenly from the mid-body position towards the aperture and aboral extremity, there is the suggestion of a collar near the aperture due to the tapering ending prior to the apertural opening (Fig. 32a). In some specimens there is an apparent lateral compression, but it is usually slight and probably related to the fragility of the structure. It has a well defined outline, and the arrangement of flattish pieces of quartz give it a smooth surface. A network of organic cement is seen at most junctions of these particles (Fig. 32c). The mesh is about 280–350 nm in diameter and the walls 350 nm thick (Fig. 32d). The aperture is circular with often a rugged outline due to the placement of the flattish particles (Fig. 32b).

MEASUREMENTS (in μm). Based on ten specimens: body length 77–95, breadth 39–55, diameter of aperture 20–27.

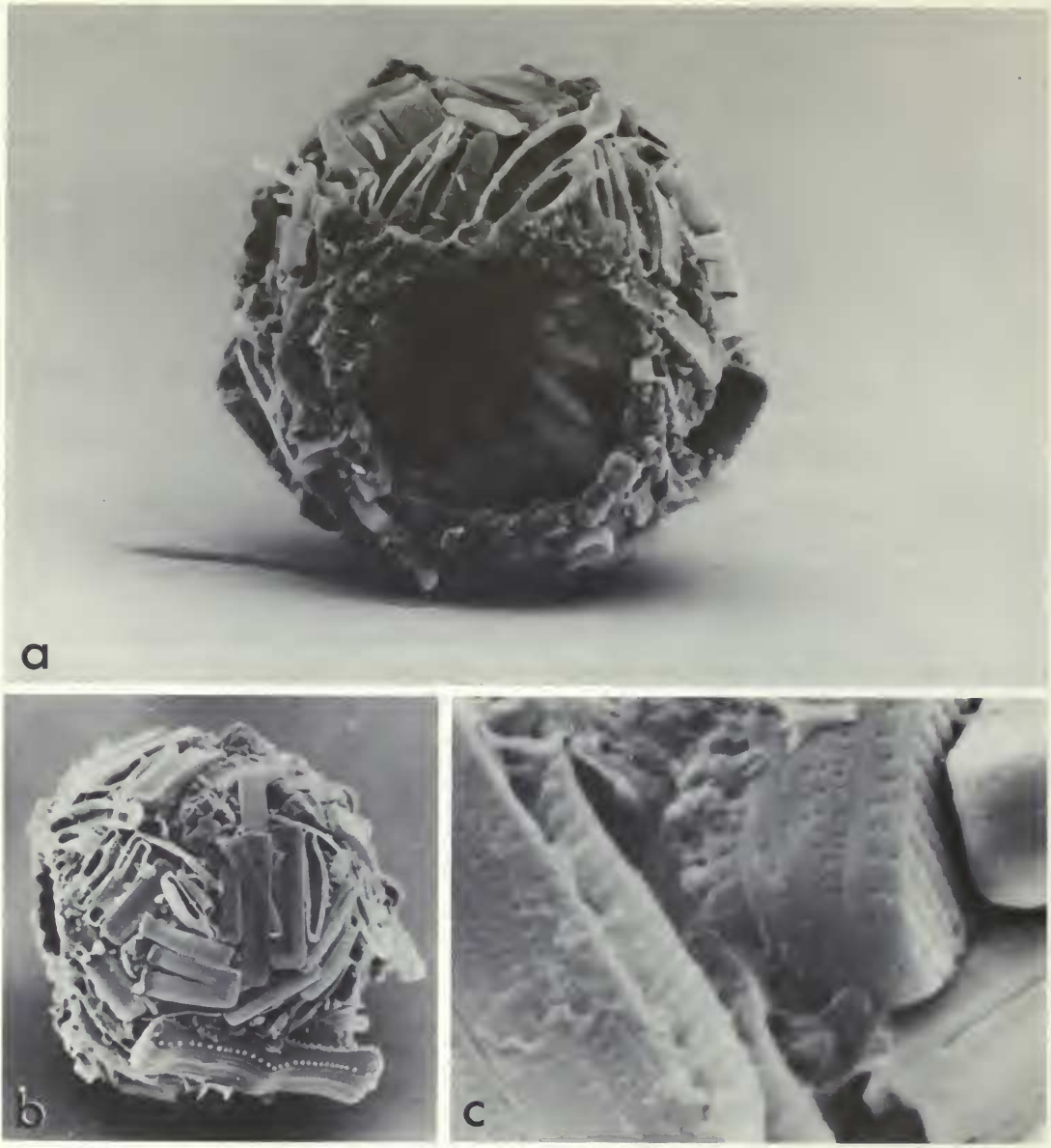

Fig. 31 *Difflugia angulostoma:* a, apertural view ×1600; b, lateral view, note the covering diatom frustules ×1000; c, shell surface with strands of organic cement ×8700.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Myndd Hiraethog, Denbigh, Clywdd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Australia (Playfair, 1918), Germany (Levander, 1894), Roumania (Godeanu, 1972).

REMARKS. Levander (1894) described four different forms of *D. acuminata,* one of which–type 'b'–was considered by Playfair (1918) to represent a distinct species., *D. levanderi.* Both of these authors suggested that there were two sizes of these specimens, '110×60 and 70×40 μm', the larger being rough and 'stony' whilst the smaller were chitinous with small, scattered granules. Recent descriptions of *D. levanderi,* for example

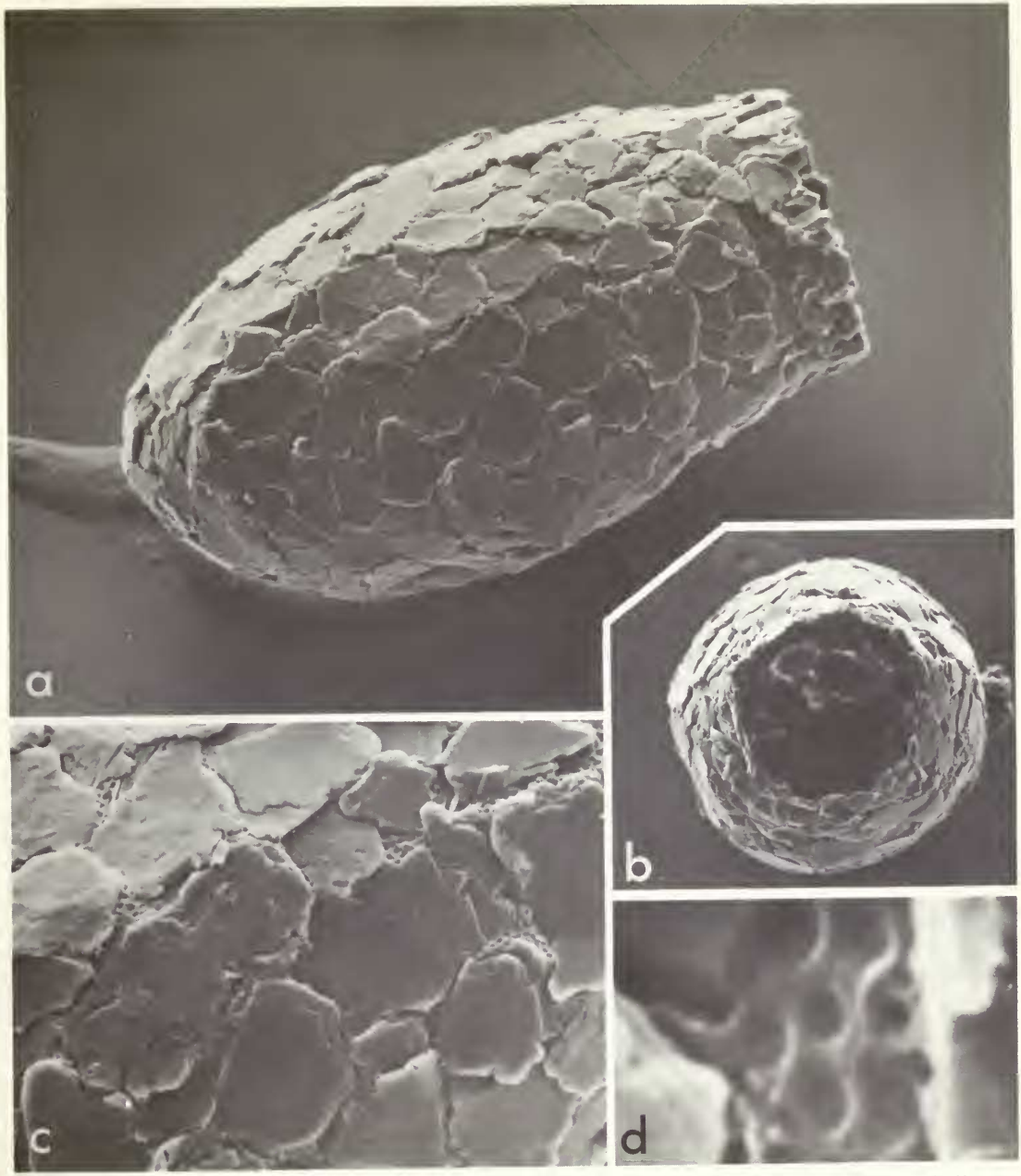

Fig. 32 *Difflugia decloitrei:* a, lateral view ×1300; b, apertural view ×900; c, portion of shell to show arrangement of flat particles to give a smooth surface ×2400; d, detail of organic cement network ×22 000.

that given by Gauthier-Lièvre & Thomas (1958) stated a range of body length of 85–140 μm suggesting that these are the larger specimens of the earlier authors. The specimens described by Godeanu (1972) as *D. decloitrei* appear to be similar to the group of smaller specimens, having a similar structure and large aperture. Those described here are in good agreement with this latter description and share similar measurements; body length 62–86, breadth 40–56 and diameter of aperture 20–23 (Godeanu, 1972). In the absence of larger shells for comparison the present specimens are referred to *D. decloitrei*.

Difflugia gramen Penard, 1902

This species has recently been redescribed (Ogden, 1980), but is included here because the numbers examined allow a comparison of dimensions between specimens from different habitats and localities. Both samples were collected in August, 1979, from sites which are about fifty miles apart. Specimens 'A' were selected from a sample of algae and water plants in stationary water (see Ogden, 1980), specimens 'B' from aquatic plants at the banks of the River Brett, near Hadleigh Suffolk, which in summer is a slow moving, small watercourse.

MEASUREMENTS (in μm). 'A' thirty-five specimens; 'B' forty-four specimens.

	body length	breadth	diameter of aperture	B/L	d/L	d/B
'A'	89–117	70–112	23–39	0·96±0·07	0·34±0·04	0·36±0·03
'B'	61–97	42–75	18–33	0·77±0·07	0·32±0·04	0·43±0·04
avg. 'A'	98·8	94·3	33·6			
avg. 'B'	78·7	60·5	26·2			

REMARKS. In shell construction the 'A' specimens are larger, spherical and more regular, only one aperture not appearing typically trilobed. Whilst, 'B' specimens are ovoid and nine (about 20%) had four lobes or were irregular in outline. It is interesting to note that the common feature between these specimens is the ratio of the aperture to the body length.

Difflugia masaruzzi Oye, 1958

DESCRIPTION. The shell is transparent, ovoid and composed of a mixture of flattish siliceous particles including some diatom frustules, to give a fragile structure with an irregular surface and outline (Fig. 33a). Organic cement is seen at some junctions (Fig. 33c), but there is a degree of overlapping with most particles. It appears as a network having a mesh of about 450–600 nm in diameter with walls 200 nm thick, each enclosure having a smaller network with a mesh about 90 nm in diameter (Fig. 33d). The aperture is circular, wide, usually with an irregular margin (Fig. 33b).

MEASUREMENTS. (in μm). Two specimens: body length 66–67, breadth 39–43, diameter of aperture 25.

MATERIAL EXAMINED. Specimens were collected from a sample of aquatic plants taken from the edge of a pond at Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Congo (Oye, 1958), Costa Rica (Laminger, 1973a), Mexico (Laminger, 1973a).

REMARKS. In the initial description of *D. mazaruzii* it was stated by Oye (1958) to be similar to *D. rubescens* and *D. lucida*, although it only shares a transparent shell with these two species. The present specimens agree well with his description of a shell having some large distinct particles attached, and an aperture devoid of a regular margin more or less wavy because parts of the shell extend to the edge. Two specimens formed the basis for the earlier report and were somewhat larger, 72 and 78 μm in body length, 44 and 55 μm in breadth, 28 and 30 μm diameter of aperture. Although this species is similar in size to *D. glans* Penard, 1902 (see p. 7), it is distinct in having a transparent, fragile shell, wide aperture and a patterned organic cement.

Difflugia mica Frenzel, 1892

DESCRIPTION. The shell is brown, spherical or ovoid with a shallow apertural collar (Fig.

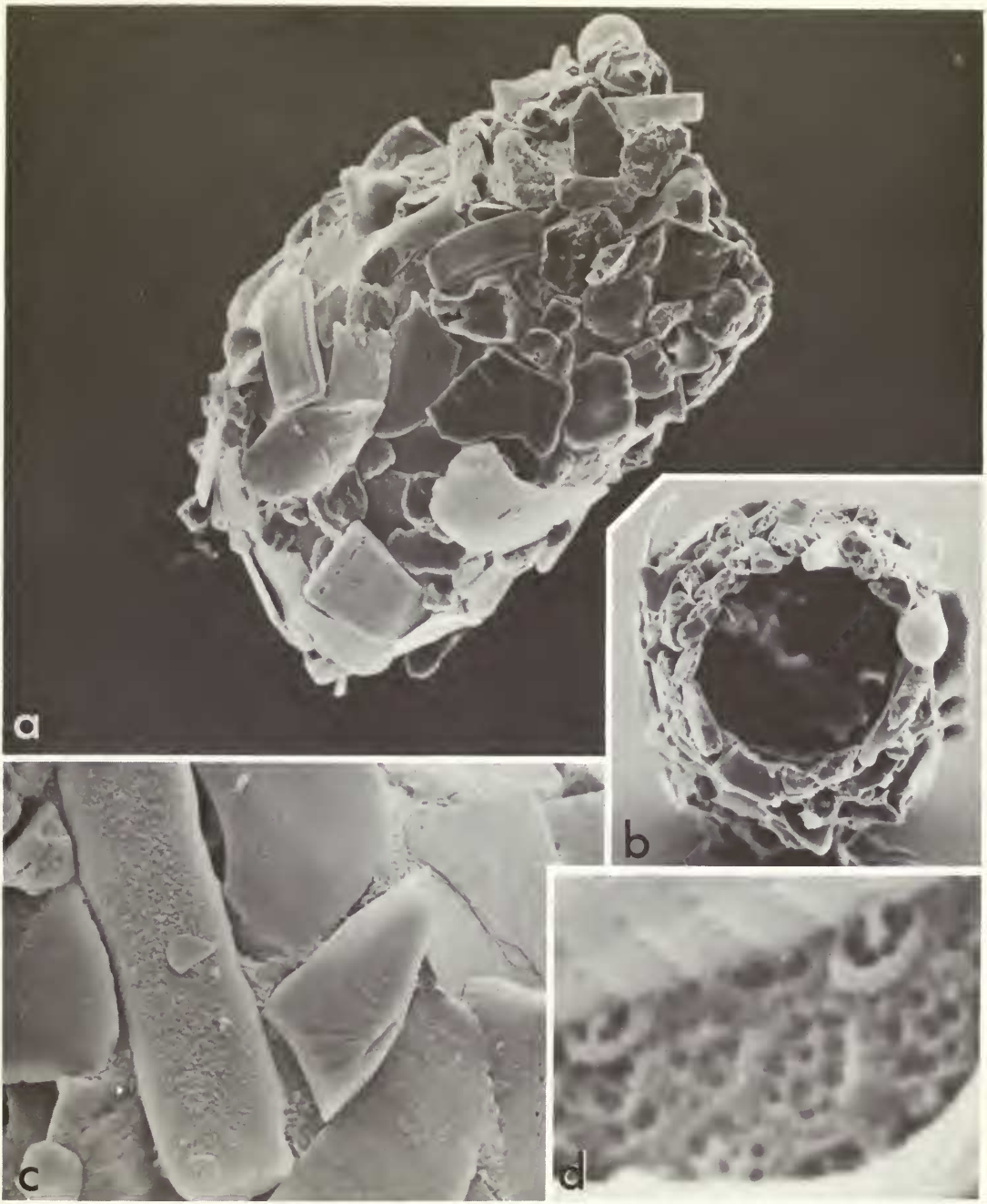

Fig. 33 *Difflugia masaruzii:* a, lateral view ×1400; b, apertural view ×1100; c, shell surface illustrating the distribution of organic cement ×4200; d, detail of organic cement network ×26 000.

34a). It is composed of small flattish pieces of quartz (Fig. 34d), packed tightly together to form a strong structure with a smooth surface and positive outline. Only small strands of organic cement are visible between the particles (Fig. 34e). The aperture is circular and usually well defined by the collar, which has a thin, even layer of organic cement around it

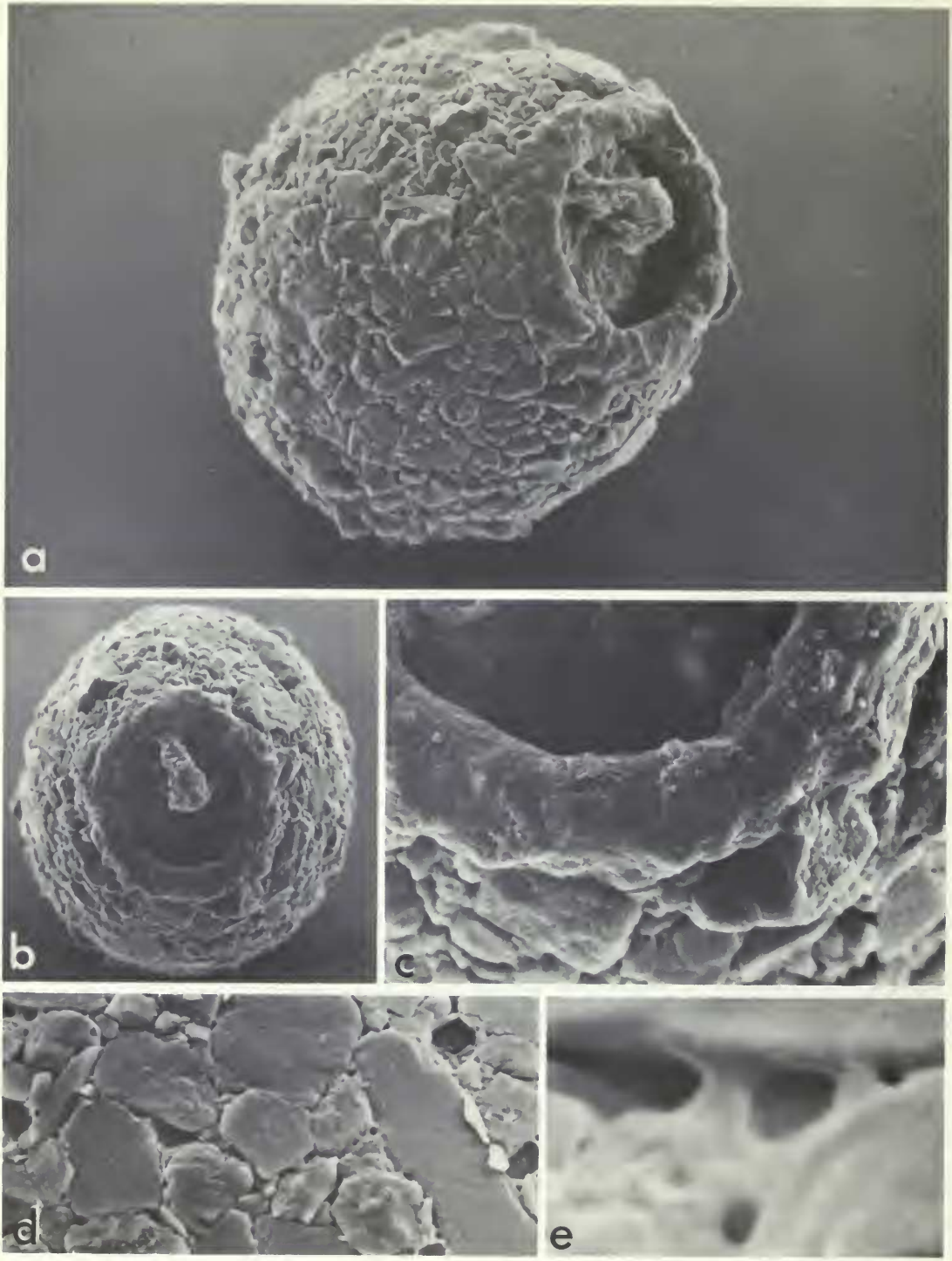

Fig. 34 *Difflugia mica:* a, latero-apertural view showing the shallow collar ×1600; b, apertural view, note that the aperture is blocked by a cyst plug×1100; c, portion of apertural collar to illustrate the organic cement covering ×3900; d, shell surface with close packing of particles ×3800; e, detail of organic cement ×24 000.

(Figs. 34b & c). The illustrated specimen has a broken cyst membrane, made mainly of organic cement, just inside the apertural opening.

MEASUREMENTS. (in μm). Based on seven specimens: body length 44–58, breadth 36–49, diameter of aperture 12–18; B/L 0·81 ±0·10, d/L 0·31 ±0·05.

MATERIAL EXAMINED. Specimens were collected from a sample of aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk, in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Argentina (Frenzel, 1892), Germany (Schönborn, 1962*a* & *b*, 1965), Poland (Moraczewski, 1961, 1965); Roumania (Godeanu *et al.*, 1973), Switzerland (Penard, 1902).

REMARKS. This species was initially described as *Difflugia* sp. by Frenzel (1892), the specific name being added as a footnote (p.135). In redescribing the species Penard (1902) used the name *D. mica?* Frenzel, the query has been dropped by subsequent authors and the name considered to be valid.

Difflugia microstoma (Thomas, 1954) comb. nov.

Difflugia globularis var. *microstoma* Thomas, 1954

DESCRIPTION. The shell is ovoid or subspherical, composed mainly of a mixture of small to medium pieces of flattish quartz and diatom frustules. The particles are arranged to give a relatively smooth outline (Fig. 35a), with the diatom frustules being in general additions to the main structure (Fig. 35d). The close packing of materials is such that only small strands of organic cement are seen (Fig. 35c). The aperture is circular and usually surrounded by a border of small particles (Figs. 35b & e).

MEASUREMENTS (in μm). Based on fifteen specimens: body length 76–105, breadth 63–83, diameter of aperture 18–29; B/L 0·79 ±0·07, d/L 0·26 ±0·03.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in July, 1978; March, 1980 and at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), France (Thomas, 1954).

REMARKS. Thomas (1954) considered when describing the variety *D. globularis* var. *microstoma* that it was similar to specimens of *D. globulosa* illustrated by Penard (1902, p. 258 Fig. 6), although he later (Gauthier-Lièvre & Thomas, 1958) proposed both as synonyms of *D. minuta* Rampi, 1950. The examples of *D. minuta* described in this report show that *D. microstoma* is distinct in having a larger ovoid shell with a small aperture (compare ratios B/L and d/L, below), the latter feature also differentiates it from *D. globulosa* Dujardin, 1837.

Difflugia minuta Rampi, 1950

DESCRIPTION. The shell is ovoid or spherical, composed mainly of small pieces of flattish quartz and the occasional fragment or diatom frustule (Fig. 36a). The particles are packed so closely, to give a robust structure, that organic cement is visible only as small strands (Fig. 36c). The aperture is small and often surrounded by a narrow lip of organic cement (Fig. 36d), the lip is not apparent in side view but makes the apertural opening distinct when viewed *en face* (Figs. 36b & d).

MEASUREMENTS. (in μm). Based on six specimens: body length 44–53, breadth 34–48, diameter of aperture 9–12; B/L 0·98 ±0·08, d/L 0·25 ±0·04.

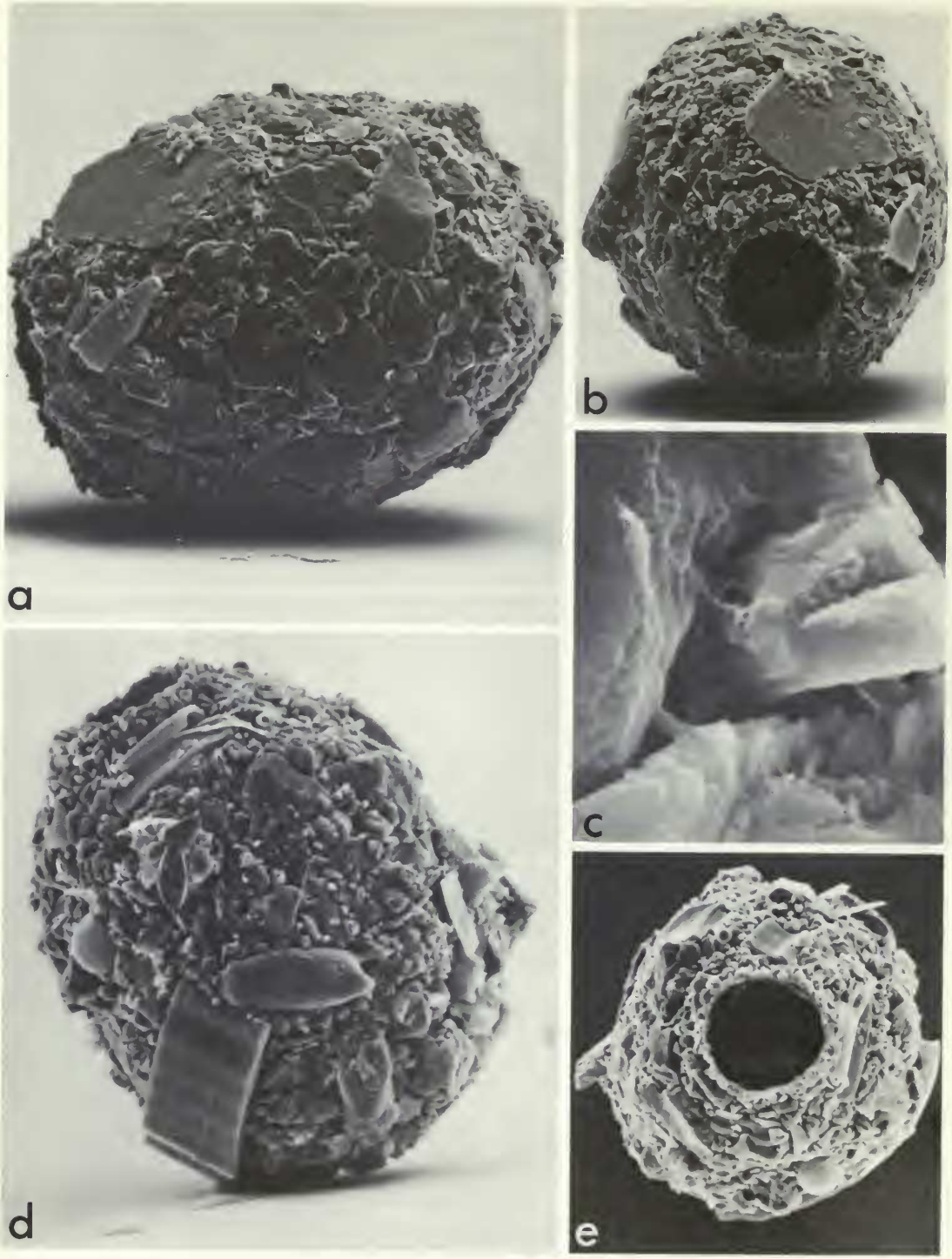

Fig. 35 *Difflugia microstoma:* a, lateral view of shell with smooth surface ×980; b, apertural view ×770; c, portion of shell surface with strands of organic cement ×13 000; d, lateral view of shell with added diatom frustules ×770; e, apertural view ×580.

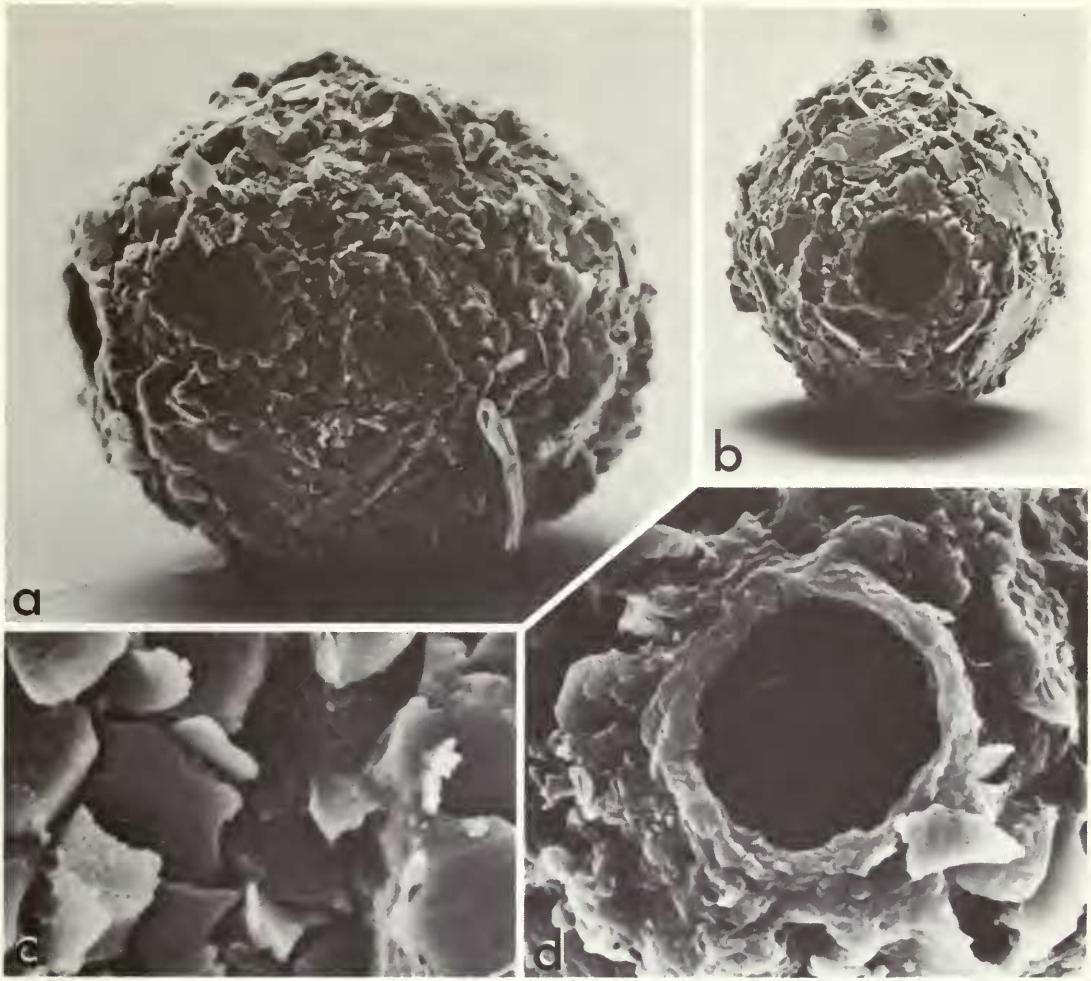

Fig. 36 *Difflugia minuta:* a, lateral view ×1400; b, apertural view ×970; c, portion of shell surface showing close packing of particles ×7700; d, detail of aperture to show narrow lip of organic cement ×3700.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at three locations, Cranes Moor, in May, 1977; Holmsley, in July, 1978, both in the New Forest, Hampshire; Myndd Hiraethog, North Wales in August, 1980; and aquatic plants taken at the bank of a pond near Burley, New Forest in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Brazil (Green, 1975), Costa Rica (Laminger, 1973*a*), Germany (Schönborn, 1965), Italy (Rampi, 1950), Roumania (Godeanu *et al.*, 1973).

REMARKS. The initial report (Rampi, 1950) of this species is brief, consisting of one figure and a few lines of description. These note that it has a globular shell made mainly of quartz particles and concludes that it differs from *D. globulosa* by its small size, length 53 μm, breadth 48 μm. Unfortunately no dimensions for the aperture are given. The specimens referred to this species by Gauthier-Lièvre & Thomas (1958) are all much larger than the measurements given by Rampi (1950), and are here considered to represent *D. microstoma* (see p. 53).

D. minuta is considered a distinct species in having a circular shell composed mainly of quartz, with a small aperture surrounded by a narrow lip or rim of organic cement.

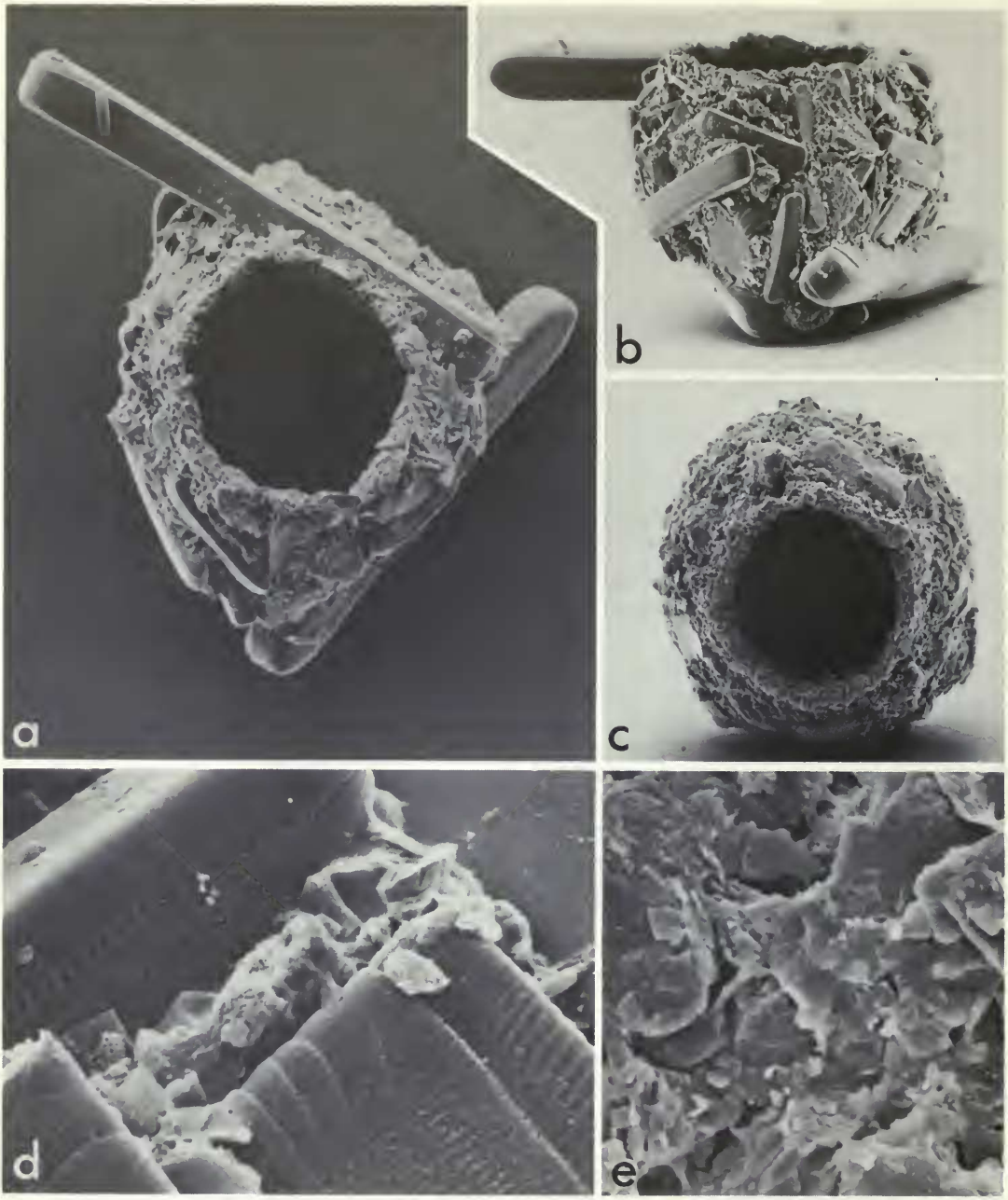

Fig. 37 *Difflugia rotunda:* a, apertural view ×270; b, lateral view ×240; c, apertural view of specimen made mainly of quartz particles, note the regular outline of the aperture ×290; d, portion of shell surface of 'diatom' specimen ×3300; e, shell surface of specimen made mainly of quartz ×2900.

Difflugia rotunda nom. nov.

Difflugia globularis var. *sphaerica* Chardez, 1956

DESCRIPTION. The shell is brownish, spherical or hemispherical, with the outline frequently distorted by the addition of large diatom frustules (Figs. 37a & b). The basic structure is made

mainly of quartz (Fig. 37c), but diatom frustules or fragments of frustules, are often mixed with this in different proportions (Fig. 37b). This material is usually packed tightly together so that only small strands of cement are seen (Figs. 37d & e). The aperture is circular, sometimes slightly irregular, but usually surrounded by a shallow rim of small particles (Figs. 37a & c).

MEASUREMENTS (in μm). Based on sixteen specimens: body length 133–204, breadth 138–193, diameter of aperture 79–113; B/L 0·98 ± 0·12, d/L 0·55 ± 0·07.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in May, 1978; March, 1979; 1980 and Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Argentina (Vucetich, 1973*a* & *b*), Belgium (Chardez, 1956).

REMARKS. In the original description of this variety, *D. globularis* var. *sphaerica*, Chardez (1956) noted that it differed in both size and diameter of aperture, the latter feature being about half the breadth, from his concept of *D. globularis*. According to Cash & Hopkinson (1909) the name *globularis* was used in error by Wallich (1864) for *D. globulosa* Dujardin, 1837. Nevertheless, these distinguishing features are used here to differentiate these specimens from other spherical species. Again a new name is proposed because the term *sphaerica* has been widely used for varieties in the terminology of this genus.

ETYMOLOGY. The specific name has been chosen to reflect the shape of the shell (L. *rotunda* = round circular or orbicular).

Difflugia stoutii sp. nov.

DESCRIPTION. The shell is ovoid or ovoid elongate, composed of mainly small, flattish particles of siliceous material, including quartz, diatom frustules and shell plates from smaller testate amoebae (Figs. 38a & d). It is extremely fragile, several specimens having collapsed in preparation, and hence the apparent lateral flattening of the specimen shown in Fig. 38c. Organic cement is seen only as small threads due to the regular overlapping of the shell components (Fig. 38e). The aperture is roughly circular, small and appears to be recessed, but this latter feature may be due to structural fragility (Figs. 38b & d).

MEASUREMENTS (in μm). Based on four specimens: body length 47–59, breadth 33–36, diameter of aperture 9–12.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1979.

REMARKS. The present specimens are similar to three species recently described from Germany, namely *D. stechtinensis* Schönborn, 1962, *D. sudiformis* Schönborn, 1966 and *D. szczepanskii* Schönborn, 1965. They differ from the two former species in general dimensions, *D. stechtinensis* is almost spherical, with an aperturual diameter equal to half the body breadth, whilst *D. sudiformis* is an elongate, very slender species. *D. szczepanskii* is a slightly larger species but differs mainly in having an aperture size two-thirds of the body width. All three species are described as having a hyaline shell covered with a meagre scattering of particles.

D. stoutii is distinct in having a fragile, elongate ovoid shell composed of flattish particles and a small aperture.

ETYMOLOGY. This species is named after the late Dr John Stout in recognition of his contributions to recent advances in protozoology.

Difflugia urceolata Carter, 1864

DESCRIPTION. The shell is opaque, ovoid or rotund, often having one or more irregular blunt

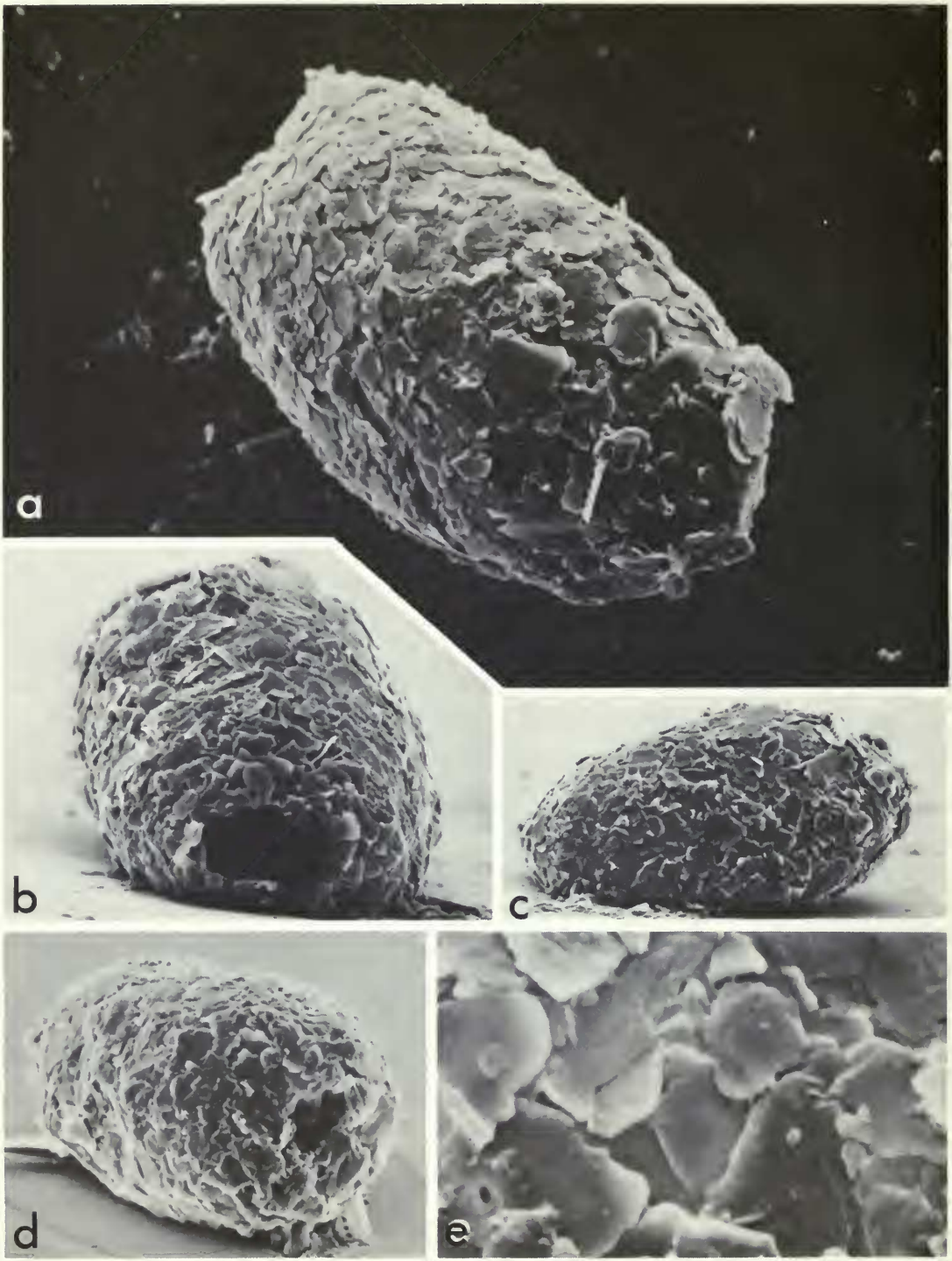

Fig. 38 *Difflugia stoutii:* a, lateral view ×1700; b, apertural view ×1700; c, lateral view of specimen slightly compressed anteriorly ×1100; d, latero-apertural view of ovoid specimen with slightly recessed aperture ×1300; e, shell surface, note the overlapping of particles ×5800.

aboral protruberances, and a pronounced apical rim or collar (Fig. 39a). The rim has a recurved appearance the edge of which is usually well defined (Figs. 39b & c), with an abundance of organic cement apparent as part of the rim matrix (Fig. 39e). The body is composed of small to medium particles of quartz, blended together so that the smaller particles and organic cement fill the gaps between the larger particles and give a relatively smooth surface. Diatom frustules or parts of them are occasionally included in the structure. Organic cement in the form of a network is seen as part of the matrix (Fig. 39d), the mesh has a diameter of about 240–290 nm with walls 100–180 nm thick (Fig. 39f). The aperture is usually circular (Fig. 39a).

Variation in this species is not uncommon. Although usually limited to the presence or absence of aboral protruberances, an occasional deformed shell may be seen. The specimen illustrated here (Figs. 40a & b) has a depressed apical rim, malformed body and defined aboral protruberances are absent.

MEASUREMENTS (in μm). Based on twenty-one specimens: body length 204–398, breadth 193–426, diameter of aperture 87–198; B/L 0·92 ± 0·10, d/L 0·44 ± 0·06.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire on several occasions, May, 1977; 1978 and March, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Boltovskoy & Lena, 1971, 1974; Dioni, 1970; Vucetich, 1973*a* & *b*), Australia (Playfair, 1918), Austria (Laminger, 1972*c*, 1973*b*), Belgium (Chardez, 1960, 1961*b*; Chardez & Gaspar, 1976), Brazil (Green, 1975), British Isles (Cash & Hopkinson, 1909; Ogden & Hedley, 1980), Chile (Decloitre, 1954), China (Decloitre, 1954), Congo (Chardez, 1964; Štěpánek, 1963), Czechoslovakia (Štěpánek, 1952), France (Deflandre 1962b; Thomas, 1954), Germany (Jung, 1936), Hungary (Bereczky, 1973), Italy (Grandori & Grandori, 1934), Java (Bartoš, 1963*a*), Netherlands (Hoogenraad & Groot, 1940), Poland (Moraczewski, 1965), Russia (Kourov, 1925), Spain (Margalef, 1955), Sudan (Gauthier-Lièvre & Thomas, 1958), Switzerland (Penard, 1902), United States of America (Laminger *et al.*, 1979), Venezuela (Deflandre, 1926*a*; Grospietsch, 1975).

REMARKS. This is one of the most widely reported specimens of *Difflugia*, probably due to its size and distinctive shape. However, variation in shell construction has led to the description of several varieties. Thomas (1954) used the presence of aboral protruberances to differentiate the variety *olla* Leidy, 1879; whilst Gauthier-Lièvre & Thomas (1958) list four which differed in rim construction, namely *lageniformis* (Wallich), *lageniformis* forma *minor* forma nov., *minor* Deflandre and *sphaerica* Playfair; and more recently descriptions of specimens which differed in shape and material have produced two more-var. *chayuensis* Wang Jiagi, 1977 and forma *subureceola* Chardez & Gaspar, 1976.

These reports of natural variation can have little value until they are thoroughly investigated, and the present specimens are therefore referred to *D. urceolata*.

Compressed species

Difflugia hiraethogii sp. nov.

DESCRIPTION. The shell is light yellow or transparent, thin pyriform with a distinct neck or collar which often has parallel sides (Figs. 41a & b). The neck region is made of angular quartz and usually has a rough appearance (Fig. 41b), whilst the remainder of the body is composed of small to medium pieces of flattened quartz and has a smooth appearance. Organic cement is frequently seen in small areas as part of the shell matrix (Fig. 41d). It is in the form of a network, made of fused rings each having an internal diameter of about 250–320 nm and walls 200–260 nm thick (Fig. 41e). The aperture is circular and surrounded by assorted particles of quartz to give it an irregular outline (Fig. 41c).

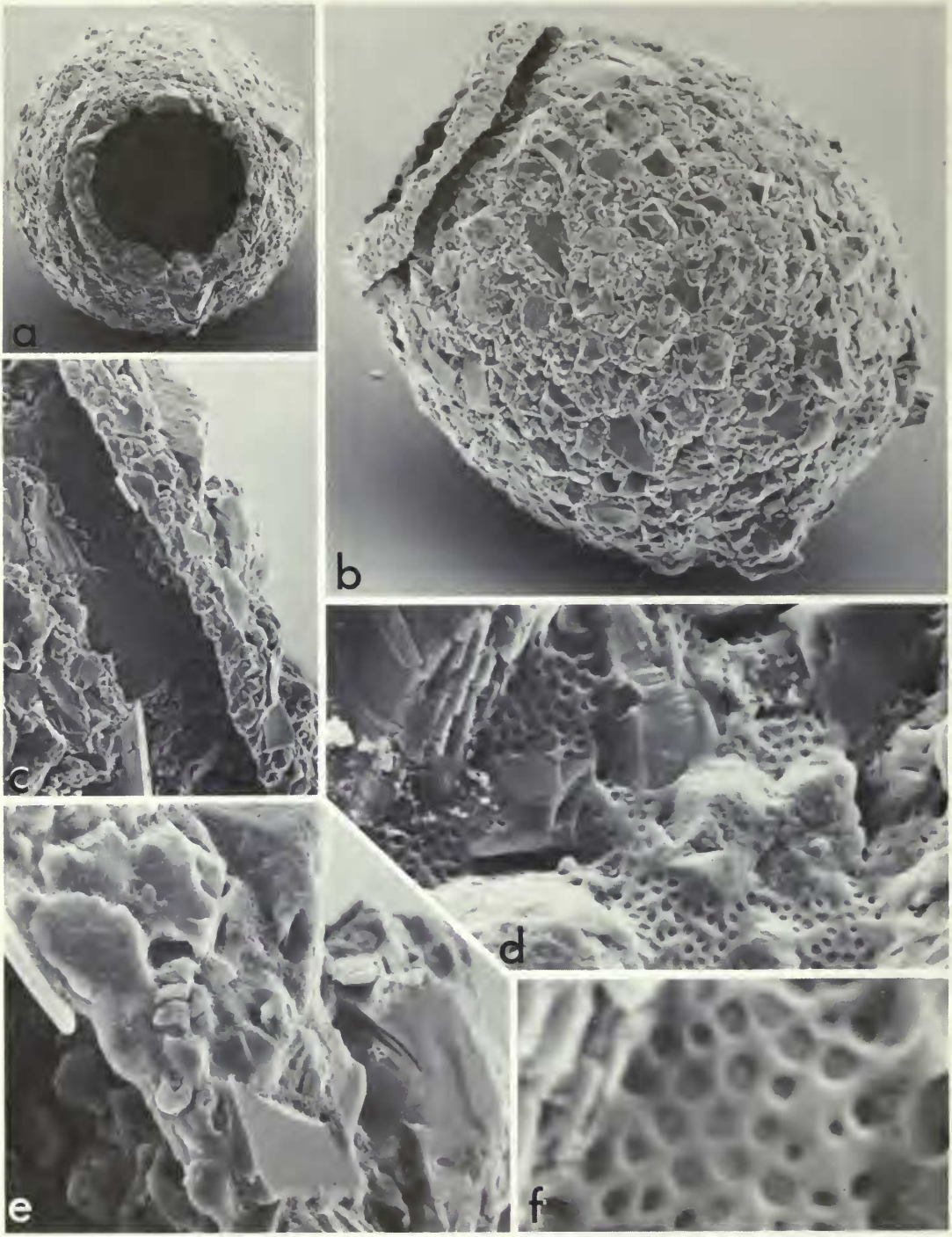

Fig. 39 *Difflugia urceolata:* a, apertural view × 180; b, lateral view, note the apertural collar and small aboral protruberances × 260; c, part of apertural collar, note the well-defined edge of small particles × 790; d, portion of shell surface to illustrate the distribution of organic cement × 5600; e, detail of apertural collar shown in c. × 3700; f, detail or organic cement network × 15 000.

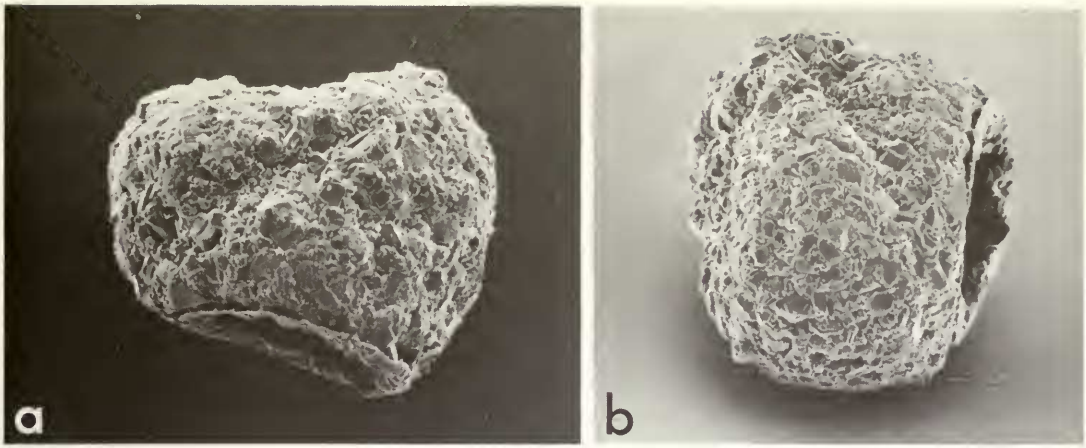

Fig. 40 *Difflugia urceolata* specimen with a deformed shell; a, lateral view ×170; b, latero-apertural view ×160.

Some of the examined specimens had cyst plugs in their apertural openings. These plugs varied from being either an uneven mixture of angular quartz (Fig. 42a) or flattish pieces (Fig. 42b), in both instances the sealing cement was similar to that binding the shell walls (Figs. 42c & d).

MEASUREMENTS (in μm). Based on twenty-six specimens: body length 137–171, breadth 87–137, depth 57–84 diameter of aperture 35–52; B/L 0·67 ± 0·06, d/L 0·26 ± 0·02.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

REMARKS. This species is similar to two other compressed species namely, *D. compressa*? and *D. lingula* Penard, 1911. Complications regarding the species *D. compressa* Carter, 1864 should have been resolved by Cash & Hopkinson (1909) who suggested that from Carter's figures he was 'beyond question' referring to a species of *Pontigulasia*. Nevertheless, the name has been used subsequently to refer to compressed specimens of *Difflugia*, either as *D. compressa* or *D. oblonga/pyriformis* var *compressa*. Whether or not there are some genuine specimens of *Difflugia* amongst these descriptions is difficult to know, but the name *compressa* is preoccupied by Carter's description and is no longer valid, and most refer to much longer, broader specimens than those described here. The present specimens are distinct from *D. lingula* Penard, 1911 and *D. lingula* var *regularis* Gauthier-Lièvre & Thomas, 1958 because these have a more rounded shape which tapers sharply from the mid-body region to the aperture, and *D. lingula* also has an aboral horn.

D. hiraethogii can be recognised by its lateral compression, distinct circular collar and aperture.

ETYMOLOGY. This species is named after the area of North Wales in which it was found.

Difflugia lucida Penard, 1890

DESCRIPTION. The shell is transparent, ovoid, gracefully curved aborally but tapering more gradually towards the aperture to give a well defined outline (Fig. 43a), and laterally compressed (Fig. 43c). It is thin, smooth and composed mainly of flattish pieces of quartz with an occasional siliceous shell plate or diatom frustule added, these particles are usually arranged so that they meet but do not overlap. Small areas of organic cement, in the form of a network, are seen as part of the shell matrix (Fig. 43d). The network is often an arrangement

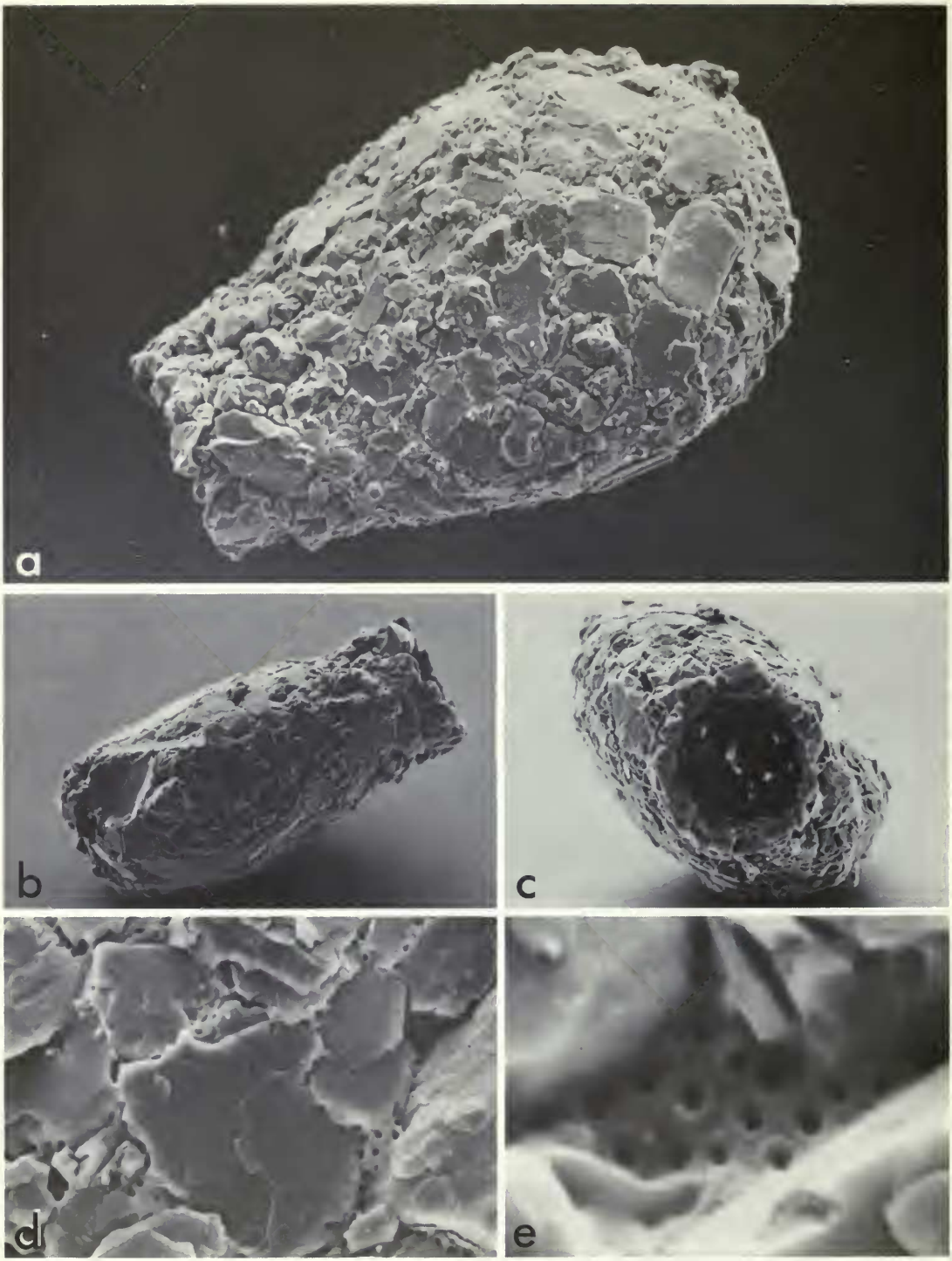

Fig. 41 *Difflugia hiraethogii:* a, lateral view ×730; b, lateral view to illustrate the distinct circular neck and compressed body ×430; c, apertural view ×540; d, portion of shell surface showing small areas of organic cement ×3500; e, detail of organic cement ×13 000.

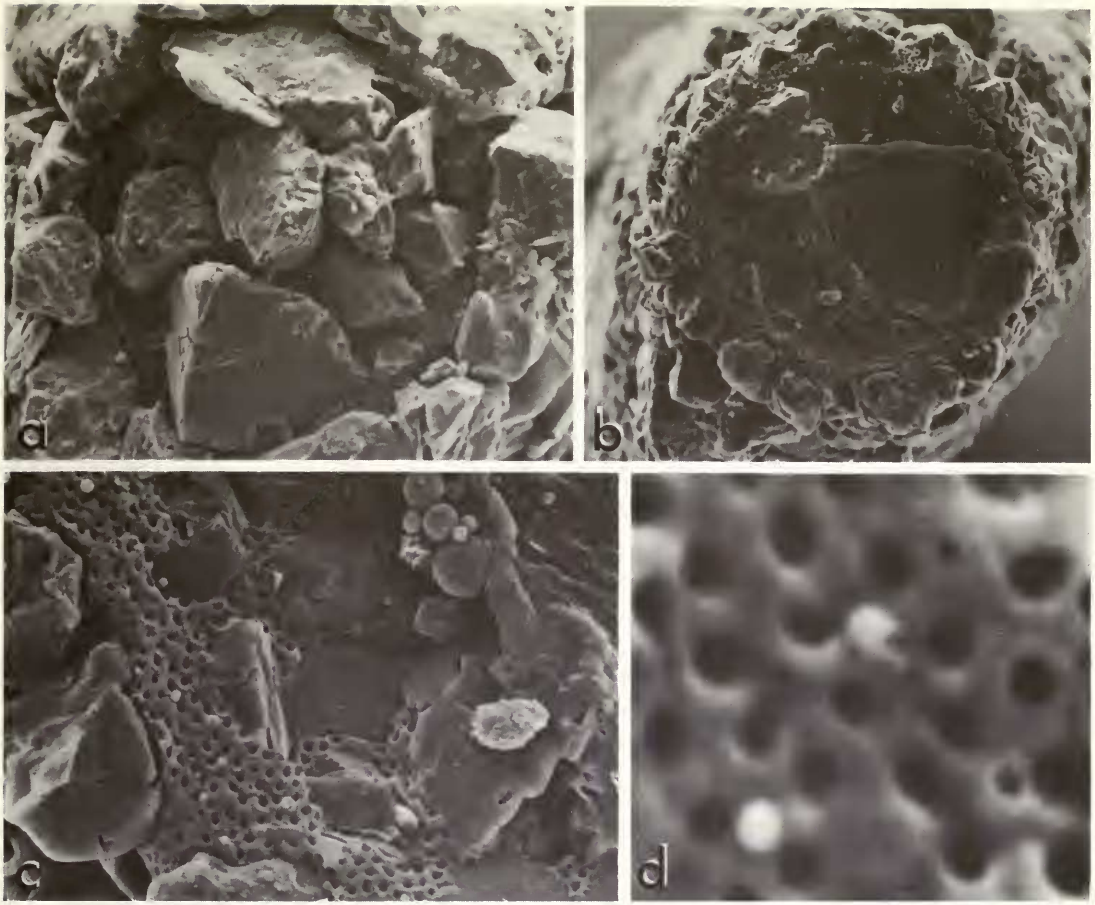

Fig. 42 *Difflugia hiraethogii:* a, detail of aperture with cyst plug composed mainly of angular quartz, organic cement at edges ×1500; b, specimen with cyst plug composed mainly of organic cement ×1100; c, portion of cyst plug shown in b., note that the particles appear to be well embedded in organic cement ×3500; d, detail of organic cement of cyst plug ×17 000.

of rings whose internal diameter is about 380–480 nm with walls 95–125 nm thick (Fig. 43e). The aperture is elliptical and surrounded by irregularly arranged particles which give a rough outline to the immediate apertural region (Figs. 43a & b).

Several presumably encysted specimens were present in the sample, and easily distinguished optically by the dark appearance around the aperture. On detailed examination this dark area was seen to be a concentration of flat particles projecting from the apertural openings (Figs. 44a & b).

MEASUREMENTS (in μm). Based on thirty-six specimens: body length 67–91, breadth 40–55, depth 23–37, diameter of aperture 23–29, depth of aperture 13–19.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* gathered at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Vucetich, 1972), Austria (Laminger, 1972*a*, 1973*b*, 1974, 1975), Belgium (Chardez, 1961*b*; Couteaux, 1969), British Isles (Cash & Hopkinson, 1909), Bulgaria (Golemansky, 1967), Canary Isles (Gracia, 1965*a* & *b*), China (Bartoš 1963*b*), Congo (Chardez, 1964; Štěpánek, 1963), Costa Rica (Laminger, 1973*a*), Czechoslovakia (Rosa, 1957; Štěpánek, 1952, 1967),

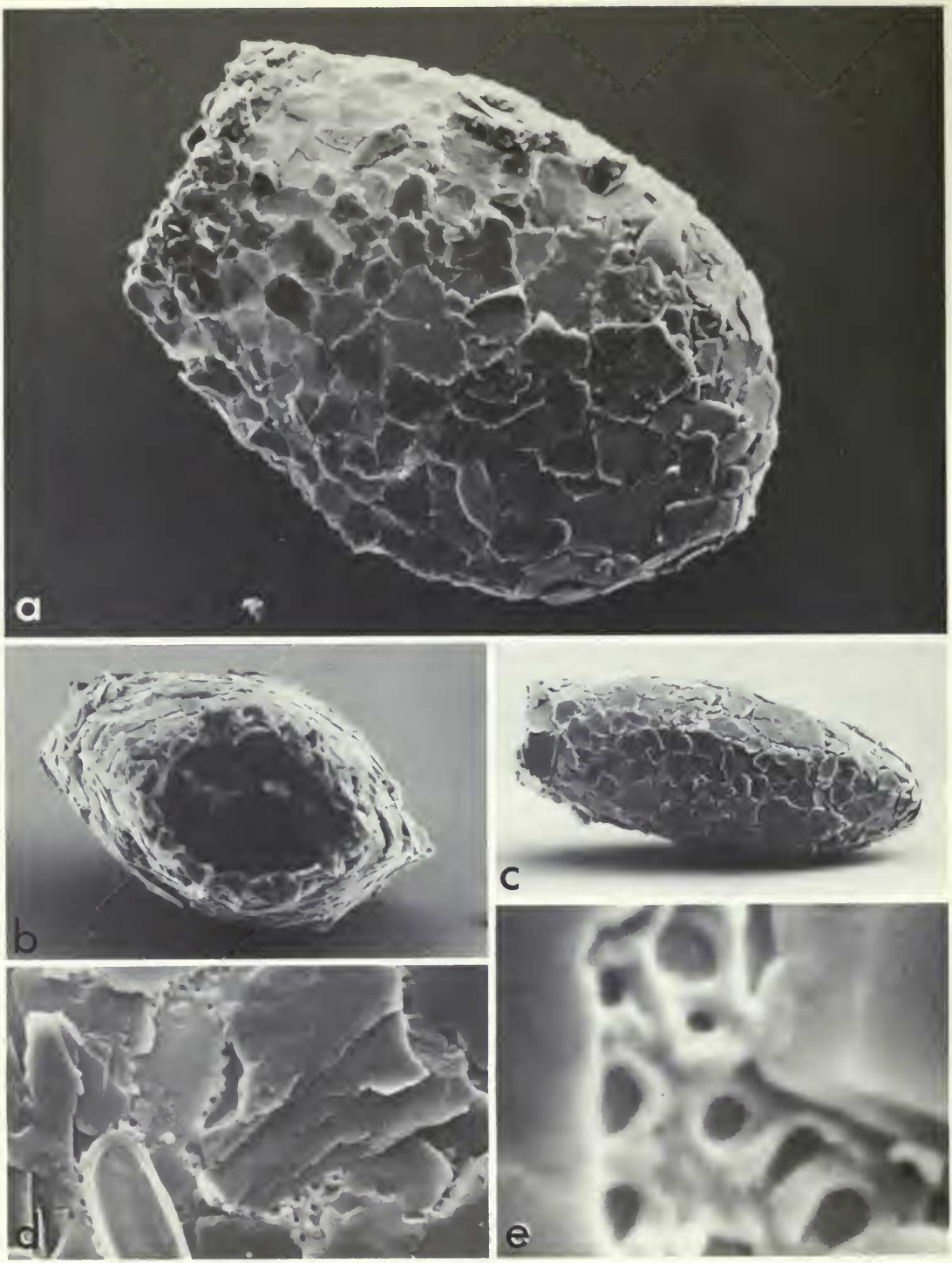

Fig. 43 *Difflugia lucida:* a, lateral view to illustrate basic outline ×1300; b, apertural view ×1100; c, view showing lateral compression and smooth surface ×840; d, part of shell surface with small areas of organic cement ×5900; e, detail of organic cement network ×23 000.

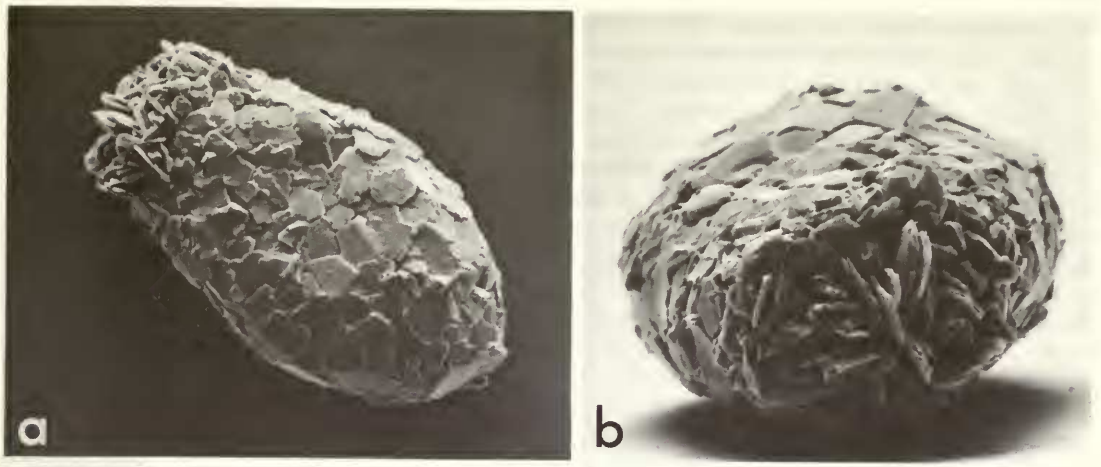

Fig. 44 *Difflugia lucida* specimen with cyst plug, note the irregular arrangement of particles in the apertural opening: a, lateral view ×620; b, apertural view × 1100.

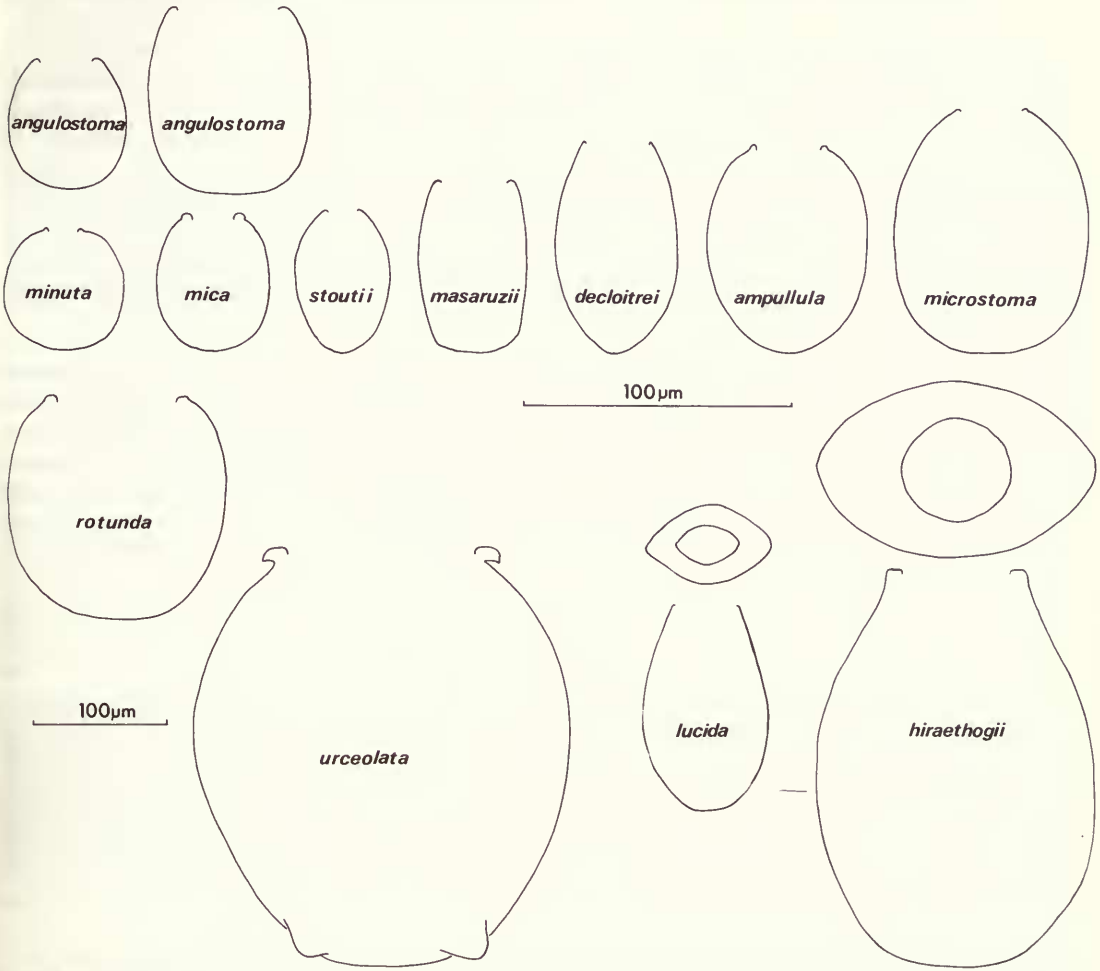

Fig. 45 Diagrams of ovoid, spherical and compressed species to illustrate the basic outline, based on measurements given in Table 4. Note that *D. rotunda* and *D. urceolata* are drawn to the reduced scale.

Table 4 Average dimensions of ovoid or spherical species and compressed species used to give basic outlines illustrated in Fig. 45

Species	Length	Breadth	Diameter of aperture	
angulostoma a.	48	45	20	
b.	68	58	38	
minuta	45	44	11	
mica	51	41	16	
stoutii	53	34	11	
masaruzii	66	41	25	
decloitrei	79	45	24	
ampululla	77	59	25	
microstoma	91	72	23	
rotunda	165	159	90	
urceolata	314	283	143	
	length	breadth	depth	diameter of aperture
lucida	76	46	30	17×25
hiraethogii	150	104	67	41

France (Thomas, 1954), Germany (Schönborn, 1962*a* & *b*), Guatemala (Laminger, 1973*a*), Hungary (Varga, 1963), Italy (Grandori & Grandori, 1943; Rampi, 1950), Java (Bartoš, 1963*a*; Hoogenraad & Groot, 1940*b*), Mexico (Laminger, 1973*a*), Morocco (Decloitre, 1961), Nepal (Laminger, 1972*b*), Netherlands (Hoogenraad & Groot, 1940*a*), Poland (Golemansky, 1970; Pateff, 1926), South Shetland Isles (Smith, 1972), Spain (Gracia, 1964), Switzerland (Penard, 1902).

Remarks. Some differences in dimensions are worth noting from earlier descriptions; Penard (1890) gave a range of body length 50–70 μm, but later stated that specimens ranged between 50–60 and rarely greater than 65 μm (Penard, 1902), Cash & Hopkinson quoted 60–80 μm, whilst Gauthier-Lièvre & Thomas (1958) suggested that there might be three groups (a) 44–50 (b) 55–70 (c) 83–90. In the present group of specimens only seven are outside of the range 70–80 μm and they are remarkable for their similarity.

This species is distinct in having a well defined shape and by being evenly compressed.

Discussion

One of the main difficulties encountered in trying to identify specimens of *Difflugia* is due to the irregular shape of the shell. It is a problem shared with other agglutinate species of protozoa, such as the foraminifera. In general most species have a regular basic outline, which may be altered by either natural variation or obscured by the addition of extraneous material. Both natural and additional variation are probably related to the composition of the shell, fragile shells being more likely to be influenced by disturbances in the environment during or after construction, whilst robust shells may be so encrusted by particles that any resemblance of a specific shape is lost.

Fragile shells are usually made of small particles arranged in a single layer and often have organic cement as a major component of the shell matrix. In some species a smooth surface composed of flattish particles is constructed, for example *D. mamillaris,* where variation in

general shape is frequently seen especially in the aboral region (see Fig. 23). Nevertheless, in a species with a similar surface but different shape, *D. lanceolata* which is rounded rather than pointed in the aboral region, there is a relatively constant shape. In the present report a third of the specimens of *D. mamillaris* differ from the basic outline given in Fig. 29, whilst all of the specimens of *D. lanceolata* agree with the outline in Fig. 18. Although robust shells are usually made of angular quartz which do not lend themselves to being arranged in a regular manner, if enough specimens of a species is present in a sample it is possible to illustrate a basic outline. The problems of subsequent recognition of such species from the basic outline is complicated when the diagnostic feature is obscured by the arrangement of particles. For instance the diagnostic feature may be the presence of a neck, but if this is hidden it may be identified incorrectly. Amongst species with this type of shell, examples of specimens incorporating a single large particle with similar dimensions to the whole shell have been observed and a not infrequent sight is to see two similar shells united. In these latter instances the shell is usually of similar size and composition, but these are not necessarily species of *Difflugia* but can be other agglutinate forms like *Pontigulasia* (pers. observation).

To assist in resolving the question of what represents the basic outline in the species described here, three sets of line drawings are provided (Figs. 18, 29, 45) which are based on the average dimensions of the specimens examined.

In the previous studies on pyriform species of *Difflugia* it has been suggested (Ogden, 1979) that measurements are useful in distinguishing species, with the body length and diameter of aperture perhaps being the more stable dimensions. However, it was emphasised that these features alone are not usually sufficient to warrant specific diagnoses. The problem of using dimensions as a diagnostic character is that they may be valid for a proportion of species in a genus, but do not hold for all especially in the present instance with a genus supposedly comprised of over three hundred species. Possibly this is best illustrated by the variability in size exhibited within a species of testate amoebae, the smallest often being reported as half the size of the largest, which does not pose problems of identification when the body length is under 80 μm, but for those of larger dimensions the difference between 200 μm and 400 μm can often be interpreted as representing two separate species. The extreme example is as we have noted previously (Ogden & Fairman, 1979) the range of measurements quoted for the body length of *D. oblonga,* 60–580 μm, which is so variable that it could embrace most of the genus or almost all of the described testate amoebae. Nevertheless, there are examples of consistent dimensions within a species, for instance those of *D. lanceolata* and *D. mamillaris* described here are in good agreement with previously published results (Penard, 1902; Grospietsch, 1957). The regularity of body length in *D. lanceolata* is such that over 87% of the specimens fall within a range of ± 10% of the average value given in Table 2, whilst in *D. mamillaris* 96% fall within the same range.

Ovoid or spherical specimens of *Difflugia* present the same problem. In certain cases groups of similar species may only be distinguished by dimensions, for example *D. anchlora, D. gramen* and *D. lobostoma* (see Ogden, 1980) which may represent a phylogenetic series. Whilst is other cases, like the *D. globulosa/globularis* species complex, size variation is so great that it is difficult not to include any ovoid or spherical specimen between 50–150 μm in this complex. Part of the difficulty is illustrated by the two groups of specimens described here as *D. angulostoma* (p. 47), where the shells are identical in construction and essentially they share the same shape, but there are differences in dimensions especially the diameter of the aperture. It is possible to separate some of these small spherical species using the latter feature in addition to other differences, as shown in the descriptions of *D. minuta, D. mica* and *D. microstoma* (see p. 53, p. 50 & p. 53). Structural differences in basic outline as mentioned earlier are mainly related to shell components and deformities, the former concerns the choice of materials and will be dealt with later, but the latter using *D. urceolata* as an example may be due to its large size. Perhaps it is easier to understand if one considers that in all probability the shell components are not cemented together until the final shape

has been moulded by cytoplasmic movements. As this process takes about sixty minutes in a small siliceous species (Ogden, 1981), it will probably take considerably longer in a larger animal, during which time in a natural environment there is a continual motion and hence a possibility of disruption. The result of such a disturbance may produce the shell illustrated in Fig. 40, sufficiently different from normal but not enough for the animal to abhort and discard the shell prior to the final stiffening of the cement.

Studies on clonal cultures of both siliceous and proteinaceous species (Ogden, 1981 & pers. observations) show that variation in dimensions are small, differences outside the norm usually being attributed to abnormal development and even here it is usually below 5%. Such abnormal development is thought to be associated with cultural differences and not a frequent natural occurrence. One feature of siliceous species behaviour which may explain some changes in dimensions, is the occasional production of a shell having a double complement of shell plates (Hedley & Ogden, 1973). However, this results in an increase in volume of an ovoid structure, which means that the enlargement in body length is probably no greater than a third.

At present there are only two reports (Jennings, 1916, 1937) on the development of *Difflugila corona* in the laboratory. Both have shown that there can be some variation in shell construction and until further observations are available on other species of *Difflugia*, the question of shell size and composition as diagnostic features will remain a subject of speculation.

Mention has already been made in the literature of differences in shell construction and the three categories which are readily identified, robust, intermediate and fragile (Ogden, 1980). But the choice of materials, other than a comment (Ogden, 1980) on the influence of pH, has not been discussed. That a system of choice is available to the animal is clearly demonstrated by the composition of certain shells. For example, *D. minutissima, D. lanceolata, D. mamillaris* and *D. decloitrei* all use flattish pieces of quartz, in some instances small flat particles of diatom frustules may be substituted, but the components used appear to be restricted in size and thickness. The function of the cytoplasm to identify and select these particles may appear to be extreme. Nevertheless, it can be measured against the ability of siliceous testate amoebae to hold each shell plate during shell construction, place it in position so that there is an even amount of overlap between plates and in some specimens manipulate spines into definite positions (Ogden, 1981). This selectivity is not restricted to flat particles, but probably includes the choice of diatoms or angular particles, as well as mixtures of all types in the composition of *Difflugia* shells. An additional factor that influences the choice of particles is undoubtedly the structure and extent of organic cement in the shell matrix.

It has already been suggested (Ekert & McGee-Russell, 1974) that the organic cement which binds the shell particles together in *Difflugia lobostoma* imparts both strength and flexibility to the structure. This may seem obvious from the different type of shells constructed by these animals, but it has an importance related to the material used. For instance, when the cement becomes part of the surface matrix, usually in species with flat particles, it is found at each facet as part of the shell wall. The strength of the shell is then directly related to the tenacity of the cement at these junctions.

Furthermore, in species where there is some overlapping of particles the cement is interwoven with the material and can be likened to the structure of a brick wall, in which the strength is dramatically increased by the combination of bricks and mortar beyond the strength of the individual materials assessed on their own. The importance of the organic cement in shell structure is easily demonstrated by treating a robust individual with either a chelating agent or concentrated sulphuric acid, in each case within a short time it is reduced to a small residue of particles. Strength is not directly due to the composition of the acid mucopolysaccharide material that forms the basic organic cement, but to the properties of this material. It has already been shown that inorganic elements incorporated with this type of material in the proteinaceous shells of testate amoebae (Hedley *et al.*, 1976; pers. observ.)

and areanceous foraminifera (Hedley, 1963) are thought to strengthen the shell. Some specimens of *Difflugia* have been examined by X-ray microanalytical techniques (pers. observ.), and found to have a significant amount of ferrous iron associated with areas of organic cement. This probably accounts for the reports of yellow or brown specimens, the degree of colouration being proportional to the amount of inorganic elements bound to the organic cement. There is no doubt that the density of this colouration in proteinaceous specimens can be used as a measure of the degree of reinforcement that the inorganic elements impart to the structure, newly formed shells being light coloured and fragile, whilst older shells are dark and strong. This measure can probably be applied to agglutinate forms as well.

The differences in the network structure of the organic cement are harder to understand, especially as the examination is limited to surface detail. A need for porosity in some of the individual organic cement units is puzzling. If they are definite pores to the interior of the shell they might function as pressure valves for aqueous interchange, because often when the animal is moving or feeding the apertural opening is completely blocked by cytoplasmic extrusions. Such a scheme could ensure that the internal volume unoccupied by cytoplasm is not isolated and allowed to stagnate. Alternatively it may be associated with the hardening process by inorganic elements. This process seems to be directly related to the environment and the chemical composition of the cement, the activities of the animal apparently having no effect on this association. The strengthening process has some degree of justification because the pores often seen between individual proteinaceous units is newly-formed, light coloured, shells of *Arcella,* are not seen in older darker specimens. Examination of the walls of such specimens show that they are thick and stronger, the implication being that the inorganic elements have strengthened the shell not the deposition of further organic material (pers. observ.).

The diversity in the construction of the organic cement units is considered to be a good taxonomic feature, although they are beyond the limit of optical microscopy, the appearance of some being particularly unique for example the button-type of *D. lacustris* (see Fig. 5e p. 9). The sharing of the same type of unit between different species may suggest some phylogenetic relationship, possibly linked to the type of shell construction whether smooth, rough, fragile or strong. However, at present only a quarter of the described species have been examined and it is too early to make proposals on such relationships. That is apart from the apparent sharing of the same organic cement pattern between most ovoid species. It is hoped that further studies in progress on this genus will help to unravel the complications attributed to describing so many different shapes and forms, and allow a comprehensive division based on shell structure.

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